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Diet, Glycogen Reserves and Resistance to Fatigue in Hatchery Rainbow Trout. Part II.[1, 2]

By the late Richard B. Miller[3]
and Frances Miller[4]

ABSTRACT

Violent or prolonged exercise increased blood lactate content of hatchery-reared rainbow trout, confirming earlier findings. In stream tests, two groups of hatchery-raised rainbow trout were planted in a mountain stream containing a resident population of cutthroat trout. One group had been raised on a fortified pelleted ration, the other on the standard raw liver diet. In 5 weeks 7.1% of the pellet-fed fish were recovered dead or moribund, and 20% of the liver-fed fish. Adverse environmental conditions (high water) did not prolong the usual two-week acclimatization period for the pellet-fed trout, as shown by cessation of mortality at the end of that time. The liver-fed trout continued to die in appreciable numbers until three weeks had elapsed. After the 2-week acclimatization period the pellet-fed trout accommodated to high-water conditions as well as or better than the resident trout in respect to blood lactate level, whereas liver-fed trout maintained a higher than normal lactate level. Ten hatchery-raised trout, 2 from the pellet-fed group and 8 from the liver-fed group, were recovered from the stream in a moribund state. These had blood lactate levels four or more times as high as the non-moribund trout on the same date. An Appendix table gives a summary of the Gorge Creek trout plantings in 1952–57.

INTRODUCTION

Miller et al. (1959) have described the preliminary work carried out in the Alberta trout hatchery in Calgary. The superiority of a fortified pelleted ration over a raw liver diet for rainbow trout was established. The advantages apparent were a lower food conversion factor and a faster rate of growth. If energy reserves are assessed in terms of liver and muscle glycogen, the pellet-fed trout are substantially better equipped to survive. Exercise by chasing for as long as 15 minutes failed to reduce the liver glycogen of pellet-fed trout. Similar exercise depleted the liver glycogen to one-half the unexercised level in the liver-fed trout, and the trout appeared thoroughly exhausted; glycogen levels were not restored after 12 hours of rest. Muscle glycogen was depleted in both groups by the exercise; it was restored by 12 hours of rest in the pellet-fed trout, but not in the liver-fed group. The build-up of lactic acid in the blood was extremely rapid during exercise in both groups. The pellet-fed group produced

[1]Received for publication May 5, 1961.

[2]At the time of my husband's death I promised to complete this paper. My son and I had hoped to "ghost write" it in his style so it could bear his name alone, but circumstances have necessitated a change in this plan.—F.M.

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substantially more lactate, possibly due to their superior store of glycogen. The observation that high oxygen consumption and high blood lactate levels persist for long periods following exercise, lends support to the hypothesis that the whole process of glycogen reduction must be entirely or almost entirely anaerobic. Of particular interest was the effect of 24 hours of exercise in a current. Liver glycogen in pellet–fed fish was reduced to about 72% of the initial value; in liver–fed fish it fell to about 30%.

The present report presents the results of stream tests carried out at the Alberta Biological Station at Gorge Creek during the months of July, August and early September, 1958; i.e., the summer immediately following the preliminary work in the laboratory at the hatchery. Identical stock raised on the two diets (a balanced diet and the standard liver–salt diet) were utilized.

EXPERIMENTS AND RESULTS

Trout Used

On October 15, 1957, rainbow trout hatched from brood stock imported from Massachusetts were 10 months old and had reached an average weight of approximately 5 g. The fish were divided into two groups, one with an average weight of 4.15 g, the other of 5.5 g. The lighter group was placed on a diet of Clark's pelleted dry rations, a complete diet; the other continued to receive the standard diet of fresh ground liver bound with common salt. The two groups were maintained on these diets until the experiment began. In May, after 212–243 days, the average weight of the pellet-fed group was 71 g and of the liver-fed group 48 g. Food conversion factors were 1.31 and 5.64 respectively (ratio of weight of food fed to the increase in weight of the fish — wet weight of liver basis). As the mortalities in both groups were similar, the pellets proved a better and more economical diet. (The bulk of the mortality in the pellet group occurred during the early period when the trout were learning to eat the pellets.)

Effect of Prolonged Exercise

Samples of blood were removed for lactic acid (lactate) analysis at the hatchery while the experimental trout were still in rectangular steel ponds. The samples were taken from 40 undisturbed trout, from 22 after 5 minutes of chasing, from 22 after 10 minutes of chasing, from 17 after 15 minutes of chasing followed by 12 hours' rest, and from 20 after 7 hours in a current of 1 mile per hour (0.45 m/sec). Equal numbers of each diet group were used for each test. Blood lactic acid was determined by the modified Barker-Summerson method (Hawk *et al.*, 1954).

On July 28, 11 pellet-fed and 9 liver-fed trout were blood-sampled when they arrived at Gorge Creek following a 60-mile trip in a tank truck.

The blood lactate contents of all these trout are shown in Table I.

TABLE I. Mean blood lactic acid content in mg% (with limits of standard error of mean), and number of fish sampled, for pellet-fed and liver-fed rainbow trout after various periods of exercise.

Exercise time	Pellet-fed		Liver-fed	
	no.	*mg%*	*no.*	*mg%*
None	20	10.8±1.4	20	9.3±1.0
5 min chasing	11	21.9±2.3	11	18.0±3.2
10 " "	11	54.3±3.3	11	31.8±4.0
15 " "	11	45.3±5.2	6	32.6±2.5
15 min shasing, then 12 hours' rest	5	6.7±1.9	5	7.8±1.5
7 hr in current of 0.45 m/sec	10	26.0±2.6	10	18.2±3.1
24 hr in current of 0.45 m/sec	10	16.1±2.5	10	17.0±1.7
60 miles in truck	11	42.7±2.4	9	46.3±2.5

THE TEST STREAM

The experiments were conducted at Gorge Creek, a fairly typical mountain stream, which flows into the Sheep River about 20 miles west of Turner Valley, Alberta. The stream was divided into Sections I, II and III (Section I being farthest downstream) using screens made of mink wire (standard mesh size) mounted on wooden frames. Each stream section was about 1300 yards long (1200 m).

Section I was poisoned July 3 to eliminate any resident trout. The wild trout in Section III were undisturbed except that a number were caught, fin-clipped and released during the summer so an estimate of their abundance could be made. Section II was to be used only as a buffer.

Heavy and prolonged precipitation during most of June and July kept Gorge Creek in constant flood. It proved to be impossible to maintain screens consistently until nearly the end of July. Unfortunately, the floods redistributed wild fish and it was found, by poisoning Sections I and II in September, that 50 large wild cutthroat and 72 small ones (not counting fry) were living in Sections I and II. Furthermore, the usual population of 300 to 400 resident wild cutthroat trout in Section III was diluted during the high waters to a calculated total of 100 fish. (The estimated population size of this group was corrected using the foregoing data, i.e., numbers of wild cutthroat from Section III recovered in Sections I and II when poisoned in September.) Consequently conditions respecting competition were not sufficiently different in Sections I and III, particularly since the wild fish were quite small and averaged about 60 g in weight. In analysing the summer's data it has proved fruitless to recognize a difference between the two sections and the results have been treated as though the two plants occupied a common enclosure with negligible competition from residents.

Plantings, Samplings and Recoveries

Sections I and III were stocked on July 28, 1958: 98 hatchery fish raised on Clark's pelleted dry rations were planted in Section I, and 98 hatchery fish raised on a liver-salt diet were put in Section III. The pellet-fed trout averaged 111.6 g (range 60–190 g); the liver-fed, 68 g (range 42–118 g). The experimental trout to be planted in the stream were weighed and tagged with Petersen-type tags several days before leaving the hatchery. Twenty untagged trout of each diet group were sent along with the tagged fish for blood and glycogen analysis at the time of arrival. This enabled the effects of the 60-mile tank-truck trip to be assessed (Table I). Hatchery-pond lactic acid and glycogen values were established in the laboratory in Calgary in May and June (Miller *et al.*, 1959).

Beginning the day after planting (July 29) blood samples were taken several times a week from pellet-fed, liver-fed and wild resident trout in Sections I and III. Excluding a few destroyed during analysis, samples were taken from 44 pellet-fed, 52 liver-fed and 78 wild trout. Once a week liver and muscle samples were collected as well (at time of blood sampling). A number of resident wild trout from portions of Gorge Creek above the experimental area were captured each week for blood, liver and flesh samples. Daily, or several times a day, patrols were made of the whole experimental area to recover dead and dying fish. A special effort was made to get samples from trout that were just on the point of death.

Unfortunately all liver and muscle samples deteriorated badly because of faulty refrigeration and no reliable glycogen values could be obtained from them. However, the bood samples taken did provide good lactic acid values (Table II).

Lactate Levels in Trout after Release in Gorge Creek

Lactate acid levels in the two groups after planting decreased markedly within 3 days' time (Table II). The two groups decreased at the same rate and at no time was there a significant difference between them, though the liver-fed group averages somewhat higher.

At planting time both diet groups had a greater level of blood lactate than the wild resident cutthroat trout. The difference was highly significant and persisted at a significant level until 15 days after planting. Thereafter, blood lactate levels were very similar in the two diet groups and in the wild trout.

During the last 6 days of the experiment, when stream conditions had returned to normal, the blood lactate level in the pellet-fed fish was only half as great as that in the liver-fed fish and was less than that in the wild fish.

The figures discussed above exclude a few fish which the stream workers were fortunate enough to find as they were dying. Ten such moribund fish consistently showed lactate levels 4 or more times as high as the apparently healthy fish taken on the same date (Table II).

Mortality in the Stream

The total pick-up of dead and moribund planted trout is shown in Table III. Observed mortality of the pellet-fed trout is 7.1%, substantially less than the 20% for the liver-fed trout.

TABLE II. Mean blood lactic acid content in mg% (with limits of standard error of mean), and number of fish sampled, for rainbow trout at intervals following planting in Gorge Creek. "Moribund" individuals are those picked up when apparently on the point of death. The first row comprises trout taken from the tank truck just before planting, after their 60-mile trip from Calgary. The last column gives values for wild cutthroat trout from the same creek.

Time after planting	Pellet-fed				Liver-fed				Wild trout	
	Healthy		Moribund		Healthy		Moribund			
days	*no.*	*gm%*	*no.*	*mg%*	*no.*	*mg%*	*no.*	*mg%*	*no.*	*mg%*
0 (in truck)	11	42.7±2.4	...	...	9	46.3±2.5	...	...	...	...
1–3	6	16.9±2.6	...	...	8	22.5±2.4	...	...	5	8.0±1.0
4–8	4	21.0±2.8	...	...	7	22.4±3.8	3[b]	74.2±22.8	4	10.7±1.1
9–15	6	15.3±2.5	2[a]	60.3±23.1	6	12.2±2.2	...	...	19	10.7±1.8
18–23	5	7.44±2.14	...	...	6	11.7±1.9	5[c]	69.1±13.9	8	10.3±1.6
28–34	10	12.3±2.1	...	...	7	11.1±1.9	...	...	22	11.2±1.1
37–41	10	5.19±0.76	...	...	10	12.3±3.9	...	...	9	8.37±0.9

[a]Range 36.2— 83.4 mg%
[b]Range 40.0—128.0 mg%
[c]Range 36.2—110.0 mg%

The pattern of death in the pellet-fed group was similar to that in other experiments, i.e., mortality tended to be concentrated in the two weeks following planting. In the liver-fed group, on the other hand, high mortality rates persisted for 24 days after planting. Of the total deaths in both groups 26 were in Section I and 27 were in Section III, thus verifying the presumption that competition was approximately equal and quite small in both sections. Also, of 10 moribund trout picked up, 8 were of the liver-fed group and only 2 had been pellet-fed. No moribund wild trout were discovered. When the stream was poisoned on September 8 and the number of fish destroyed at this time was added to those that had died or been killed for samples, 144 of the original planting of 196 fish were accounted for.

TABLE III. Dead or moribond hatchery-reared rainbow trout picked up in Gorge Creek, of the pellet-fed and liver-salt-fed groups, from July 28 to September 11, 1958. (98 trout of each group were planted on July 28, 1958.)

Time of death (after planting)	Pellet-fed	Liver-fed
days	*no.*	*no.*
0–3	4	3
4–7	2	8
8–11	3	4
12–15	4	5
16–19	0	6
20–23	0	3
24–27	1	1
28–31	0	0
32–35	0	2
Time unknown	0	7
Total	14	39

DISCUSSION

EFFECT OF PROLONGED EXERCISE

As in earlier experiments, it is evident that the blood lactate level rises during violent or long-continued muscular exercise (Table I). In both diet groups there were highly significant increases from no exercise to 5 minutes of exercise, and from 5 minutes to 10 minutes of exercise. The pellet-fed groups produced significantly greater amounts of lactate than the liver-fed trout, no doubt because of their greater stores of glycogen from which to manufacture it (Miller *et al.*, 1959). The two diet groups return to the same lactic acid level after 15 minutes exercise followed by 12 hours of rest.

Prolonged exercise in a current of 1 mile/hr (0.45 m/sec) did not produce increases in blood lactate in the surviving fish of either diet group beyond that achieved by 5 minutes of chasing. However, 4 liver-fed fish died during the current tests and one of these had a blood lactate level of 75 mg%.

The 60-mile trip by tank truck produced an increase of blood lactate to a level 4 times that of the resting fish (Table I). This is almost twice as large an increase as observed in 1957. There was no significant difference in this increase between the two diet groups, though the mean figure for the liver-fed group was 8% higher. The lactic acid level on arrival is comparable to the levels attained after 15-minutes' exercise. In 1958 oxygen was bubbled into the tank truck while the fish were in transit. This undoubtedly excited the fish and the higher lactate levels were probably the result of increased exercise.

Mortality in the Stream

The hatchery-reared trout followed a characteristic death pattern. The pellet-fed fish experienced significant mortality for 2 weeks, but almost none thereafter. Liver-fed trout continued to die in numbers for 3 weeks. A number of trout in a moribund condition were found against the screens of their particular section. They would remain in this position, completely exhausted, capable of no further effort than breathing until death occurred. No dead or moribund fish were observed among the wild resident cutthroats.

Blood Lactate During Acclimatization to Stream Conditions

At the time of planting both diet groups had a significantly greater level of blood lactate than the wild resident trout. This difference persisted at a significant level until 15 days after planting. Thereafter, blood lactate levels were comparable in both diet groups of the hatchery-reared rainbow trout and the resident cutthroat trout. In the 1957 experiment, hatchery-reared fish failed to achieve the low lactate levels observed in resident trout until 30 days after planting.

Effect of High Water on Blood Lactate

In 1958 all fish were maintaining life in a stream that was in flood until late on in the summer. Exposed to these adverse conditions, the pellet-fed hatchery-reared trout appeared to fare as well as the resident trout after the intial 2-week period of acclimatization, while the liver-fed group had appreciably more lactate. During the last 6 days of the experiment, when stream conditions had returned to normal, the blood lactate level in the sample of pellet-fed trout was only half as great as in the liver-fed trout, and was less than that in the sample of resident trout.

Blood Lactate of Moribund Fish

The above comparisons exclude the moribund trout, described above, which the stream workers were fortunate enough to find as they were dying. Ten such fish consistently showed lactate levels 4 or more times as high as the non-moribund trout on the same date. This may be a further indication that mortality and high lactate levels are associated.

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APPENDIX

During the years 1950 to 1957 accurate records were kept of many environmental factors that might have a bearing on the survival of hatchery-reared trout after their planting in Gorge Creek, a typical mountain stream. These included the effect of stream temperatures and velocities, competition, and fish size. The results of the 7-year study have been recorded in Table IV.

Introduced trout always suffered their greatest mortality during the first 14–16 days after planting, therefore the study has been concentrated on this apparently critical period of acclimatization. Total mortality rates for each year of the study have been included as well. The plants have been arranged in the table in order of the initial weight of the introduced trout.

There does not appear to be any correlation between stream temperatures, velocities and rate of mortality within the limits of this experiment. (Turbidity and flood conditions began at velocities of 4.0 ft/sec.) The smaller fish may have been influenced by the higher velocities; however, the picture is not consistent.

When native fish were present, planted trout larger than 6 ounces (170 g) in weight died in only slightly smaller numbers than fish one-quarter their weight. Any advantage their larger size might have given them over the smaller resident population appeared to have been eliminated by their inability to find niches.

When competition of native trout was eliminated, trout 1.4–1.6 ounces (40–45 g) in weight survived in markedly larger numbers than trout 6.3 ounces (79 g) in weight. The total mortality of the former was reduced to approximately one-fifth. The resident population averaged 2.6–3 ounces (74–85 g) in weight. This has suggested that trout larger than this size may be too large for this particular stream.

The eight years of experimental work with hatchery-reared trout may be summarized as follows:

A) The Influence Exerted by External Factors in the Environment

1. Water temperature. Within the limits of the experiments undertaken this factor appeared to have little influence.

2. Water velocity. Mortality rates in Beaver Creek, a stream which has a gentle flow, were much lower than in Gorge Creek, a typical mountain stream. Mortality rates were still lower in lakes with static water (Miller *et al.*, 1959).

TABLE IV. Mortality of hatchery-raised trout planted in Gorge Creek over 7 years, in relation to their size, the presence of resident cutthroat trout, stream temperature and stream velocity. Fish planted were rainbow trout except as noted. Turbidity and flood conditions begin at a stream velocity of 4.0 ft/sec.

Year	Stream section	Trout planted	Av. weight		Resident cutthroat trout			Range of stream conditions during first 16 days		Mortality	
								Maximum temp.	Water velocity	First 16 days	Total
		no.	oz	g	no.	oz	g	°F	ft/sec	%	%
1957	I	200	6.7	190	300	2.6	74	56.3–63.8	2.9–3.5	26.5	42.0
1957	II	200	6.3	179	None	...	..	56.3–63.8	2.9–3.5	29.5	46.5
1950	I	199	6.4	182	300	3.0	85	40.8–55.7	3.4–4.4	16.5	31.0
1955	II	86[a]	5.4	153	340	2.6	74	57.0–61.7	3.0–3.4	15.2	54.6
1952	...	189	3.1	88	300	...	..	50.8–60.7	3.3–4.0	61.4	66.5
1950	II	201	2.6	74	300	3.0	85	54.0–60.5	2.0–3.3	47.0	56.5
1955	I	113[b]	2.2	62	340	2.6	74	57.0–61.7	3.0–3.4	39.0	51.4
1954	II	121	1.6	45	None	...	..	52.3–61.0	3.0–3.3	9.1	11.5
1954	...	200	1.5	43	340	3.0	85	53.8–60.5	4.2–4.4	42.5	5.5
1956	...	181	1.5	43	None	...	..	53.3–57.8	3.5–3.8	5.0	8.8
1955	III	200	1.4	40	None	...	..	57.0–61.7	3.0–3.4	7.5	11.0
1954	I	200	1.03	29	None	...	..	53.8–60.5	4.2–4.4	11.0	15.5

[a]Brown trout (*Salmo trutta*).
[b]Eastern brook trout (*Salvelinus fontinalis*).

3. COVER. The physical nature of the stream appeared to be a limiting factor. The Gorge Creek experiments indicated that mortality rates could have been influenced by the larger trouts' inability to find suitable niches and sufficient food. The size of the resident population in a stream would appear to indicate the size of the trout the particular stream is best suited to accommodate.

4. FISH SIZE. (Based on Gorge Creek experiments only.) When competition is not a factor and when the introduced trout are the same size or smaller than the resident trout mortality rates were reduced to approximately one-fifth those encountered when the introduced stock were two to three times the size of the resident population. Trout considerably larger than the resident population must be too large for the stream and become exhausted in a largely fruitless search for resting places and food.

5. COMPETITION. (Limited to Gorge Creek experiments.) When the introduced trout raised on a salt-liver diet were approximately the same size or smaller than the resident trout, exhaustion was most severe and the greatest mortality occurred. When the individual fish of the introduced hatchery stock were substantially larger than the resident population the mortality was reduced to 10%: the influence of the resident trout ceased to be important and mortality was the same as in the presence or absence of resident trout. When the introduced stock consisted of trout 2 to 3 times heavier than the resident trout; the mortality was still very high, much higher than for smaller trout without competition.

B) THE INFLUENCE EXERTED BY THE INTERNAL ENVIRONMENT OF HATCHERY-REARED TROUT

BLOOD-LACTATE LEVELS. The 1956, 1957 and 1958 experiments at the Gorge Creek Research Station indicated that high blood lactate levels were always associated with periods of high mortality. High lactate levels were shown to be accompanied by a depletion of liver and muscle glycogen reserves. Research in many fields has proven that high blood lactate levels may be considered a measure of the extent to which exhaustion has proceeded. Extremely high lactate levels were encountered in fish that were sampled when in the moribund state that immediately preceded death. The exhaustion leading to death has been proven to be the result of the trout's unsuccessful struggle against the forces of its external environment reflected in its internal environment.

C) THE INFLUENCE OF DIET ON HATCHERY-RAISED TROUT

The 1958 experiments in the laboratory and the field indicated that trout raised on a balanced rather than a liver-salt diet may well have been endowed with sufficiently high energy reserves (in terms of stored liver and muscle glycogen) to carry them through the acclimatization period successfully, to overcome adverse external and internal environmental conditions and eventually become a self-perpetuating resident population.

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Zooplankton of Foxe Basin in the Canadian Arctic[1]

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"Calanus" Series No. 22

ABSTRACT

Zooplankton collections from 100 stations in Foxe Basin and immediately adjacent waters of the eastern Canadian arctic, made in 1955, 1956 and 1957, are considered. Available information on physical oceanography of the region is discussed, especially factors with apparent direct relationship to plankton distribution. Zooplankton standing crop on the two sides of Foxe Basin is estimated, and related to water movement, depth, ice cover and turbidity. Zooplankton quantity within the upper 50 m of the basin is estimated as about 50 mg/m^3, the western section showing approximately twice the standing crop of the eastern area. Forty-eight species of zooplankton are recorded, dominated numerically by amphipods (12), copepods (10) and medusae (9). Copepods exceed all other groups in biomass, and are represented principally by the species *Pseudatibrotus minutus*, *Calanus glacialis* and *Calanus hyperboreus*. Other especially abundant and widely spread species are *Aglantha digitale* and *Halitholus cirratus* (medusae), *Sagitta elegans* (chaetognath) and *Themisto libellula* (amphipod). From the occurrence of plankton species and apparent water movements, it is concluded that Foxe Basin is a region of opposed arctic (polar water) and subarctic (mixed polar and Atlantic water) elements, the former entering the basin from the north and dominating most of the north and central parts of the region, the latter entering from the south and influencing chiefly the southernmost part of the basin but probably extending as a minor element up the east side to the northern limits of Foxe Basin. Differences in the zooplankton development in different years are related in part to variations in duration of ice cover

INTRODUCTION

During the summer seasons of 1955, 1956 and 1957, oceanographic investigations were carried out in Foxe Basin in the Canadian eastern arctic by H.M.C.S. *Labrador*, Royal Canadian Navy, and by C.G.M.V. *Calanus*, Fisheries Research Board of Canada. Part of the work of both vessels was the collecting of zooplankton. This report includes material from all stations in Foxe Basin and in adjacent passages, Fury and Hecla Strait (northwest), Frozen Strait and Roes Welcome Sound (southwest) and northern Foxe Channel (south).

Zooplankton collecting by the *Labrador* was done between 10 July and 17 September 1955, and between 17 July and 27 October 1956, at 72 stations in the region discussed. M.V. *Calanus* collections were made between 8 September and 28 October 1955, between 6 June and 9 September 1956 and between 1 June and 9 September 1957. There were 28 stations occupied, several of them on more than one occasion. Stations occupied are shown in Fig. 1. M.V. *Calanus* stations, with the exception of one in Repulse Bay and three

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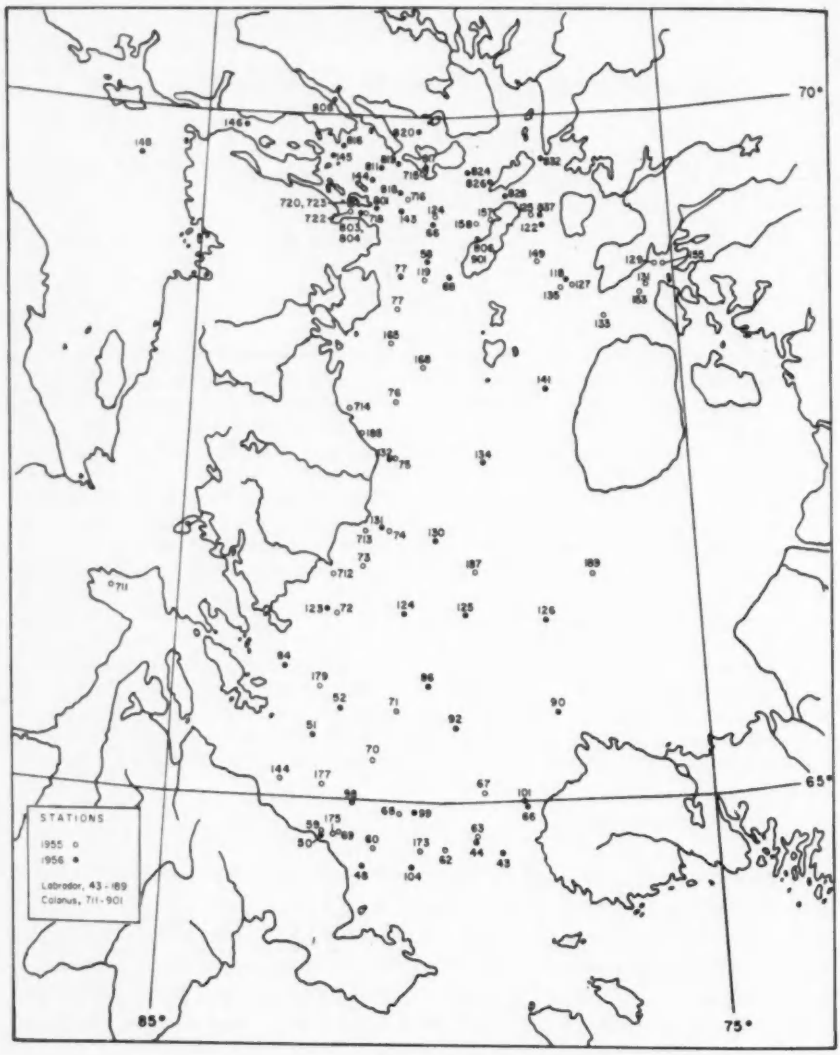

FIG. 1. Foxe Basin plankton collecting stations.

along the southern part of the Melville Peninsula coast, were limited to the northern part of Foxe Basin, from Rowley Island north. *Labrador* stations extended over most of the area of Foxe Basin (excepting the shallow, easternmost part), and also included Fury and Hecla Strait and Foxe Channel.

Previous reports on Foxe Basin plankton are few. Ross (1826) recorded *Rhachotropis aculeata* (as *Amphithoe Edwardsii*), taken during Parry's stay at

Igloolik. This chiefly benthic amphipod occurs occasionally in near-bottom plankton hauls, and was so taken by the M.V. *Calanus*. The next record of planktonic species was from Wilson (1936) who reported copepods from the east end of Frozen Strait, the west side of Foxe Basin near Cape Penrhyn and Fury and Hecla Strait. Most are predominantly benthic forms, but of the planktonic species, *Calanus finmarchicus*, *C. hyperboreus*, *Pseudocalanus minutus*, *Metridia longa*, *Acartia longiremus*, *Oithona similis* and *Oncaea borealis* are present in the M.V. *Calanus* and *Labrador* collections. Van Winkle and Schmitt (1936) recorded several decapod crustaceans from Foxe Basin, mostly benthic forms. One, *Eualus gaimardi*, occurred in M.V. *Calanus* plankton nets. Stephensen (1937), who reported collections of the Fifth Thule Expedition, included the amphipods *Anonyx nugax* from Frozen Strait, *Gammaracanthus loricatus* and *Gammarus wilkitzki* from Vansittart Island. These were also collected by the M.V. *Calanus*. A year-round series of collections from the vicinity of Igloolik, made in 1955 and 1956, was reported by Grainger (1959). There were 28 planktonic species included.

PHYSICAL FEATURES

Little information is yet available on the physical oceanography of Foxe Basin. Preliminary results of the *Labrador* cruise of 1955 (Campbell and Collin, MS, 1956) show general features of temperature, salinity and depth in Foxe Basin and Channel. From the point of view of plankton distribution, the most significant features are currents and depths (Fig. 2). Campbell and Collin (solid arrows in Fig. 2) show a near-surface flow of arctic water from Fury and Hecla Strait running southward along the west side of Foxe Basin, dividing in the southwest part of the basin into westward, southward and eastward components, part flowing out of the basin by way of Frozen Strait and Foxe Channel and part circulating into east Foxe Basin. In Foxe Channel, there is shown a continuation of the southward flow of arctic water on the west side, but a northward movement from Hudson Strait in the centre. Current direction on the east side of Foxe Channel is less clearly defined. Campbell and Collin described it as shown by solid arrows in Fig. 2. However, Dunbar (1958; dotted arrows in Fig. 2) and Campbell (MS, 1959) referred to northward moving water on the east side of Foxe Channel, and Campbell suggested an additional southward moving component close to the Foxe Peninsula shore. Regardless of the details of this, there appears to be a flow of water to the north in the eastern part of Foxe Channel. Of particular significance with regard to the zooplankton is the apparent introduction to at least southern Foxe Basin of water from Hudson Strait, and the possible extension of this influence into the eastern part of the basin. This movement allows the introduction of a subarctic element to southern and possibly to eastern and northeastern Foxe Basin, contrasting with the apparently essentially arctic condition of the west side.

Foxe Basin is, in general, a shallow sea. The deepest waters in the region discussed here are 350 to 400 m. but they are limited to a narrow strip extending from the east end of Frozen Strait to western Foxe Channel. Most of the

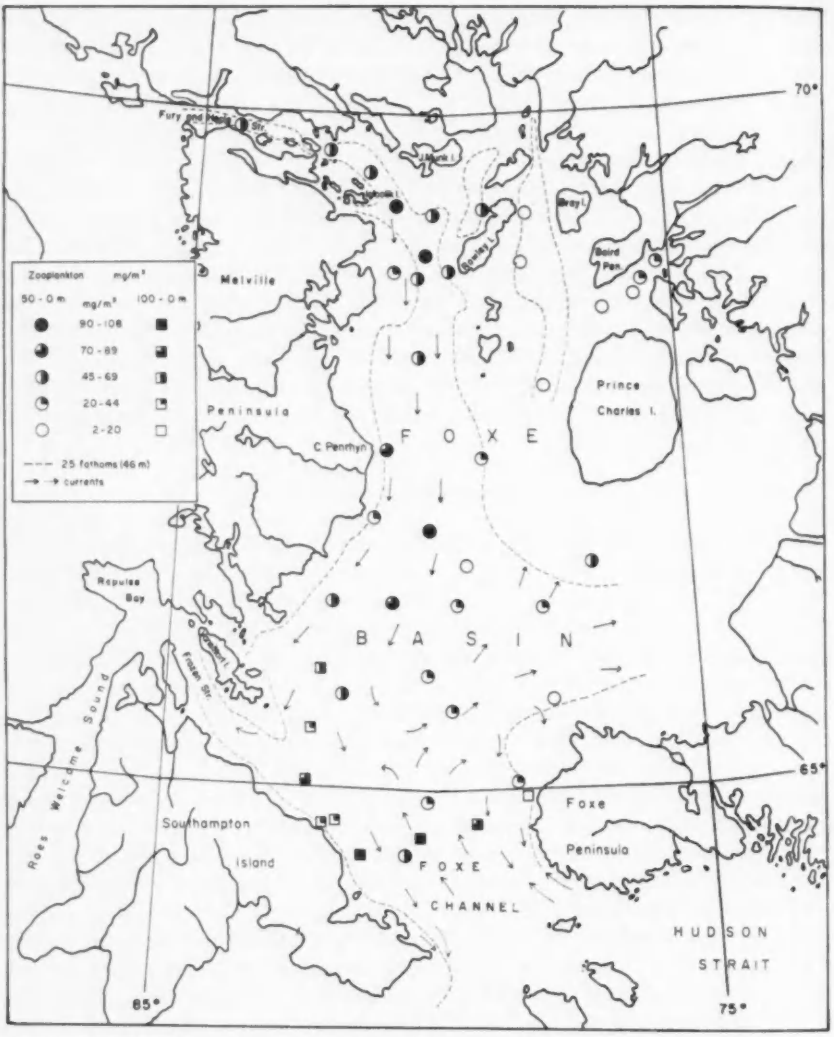

FIG. 2. Quantitative estimates of total zooplankton, bathymetry and water movements in Foxe Basin.

remainder of the basin is less than 100 m deep, and nearly all of the east side (between Foxe Peninsula and Prince Charles Island) and the northeast portion (between Prince Charles, Rowley and Jens Munk Islands) is less than 50 m deep. Depths of 100 m or more extend northward from Foxe Channel to about Cape Penrhyn, on the west side, and from the region north of Igloolik Island into Fury and Hecla Strait. An uninterrupted depth of at least 50 m extends from Fury and Hecla Strait to Foxe Channel, in the western part of the basin.

Surface temperatures, more than 0°C for only a comparatively brief period, rarely exceed 2°C at their summer maximum, according to Campbell and Collin (1956). Surface salinities, as low as about 5‰ in regions of melting ice in July and early August, were rarely less than 30‰ after that time, that is following the period of most active ice melting. Ice cover over Foxe Basin is fairly complete in winter, although usually a small open area, variably covered by drifting pack ice, persists in the northwest part of the basin (Grainger, 1959), and leads of rapidly changing character occur sporadically between the islands in the northeast section. Spring break-up begins, at least in the northwest, in late June or July, and fast ice has broken free from even the most protected bays usually by early August (although pack ice may subsequently drift back into them). The time of the breakup may vary greatly from year to year. As the only outlets from Foxe Basin are the narrow and twisted Frozen Strait and the wider but still constricted Foxe Channel, there are obvious impediments to the free flow of pack ice from the basin. Wind direction is probably the chief factor in either clearing or preventing the clearing of ice from the basin. In 1956, ice clearing appears to have occurred at about the usual time (late July or early August) in the northwest; in the northeast however heavy pack ice remained until early September, a date much later than usual, according to north Foxe Basin natives, and much later than the year previous (1955). In 1957 the northwest area, between Rowley Island and Fury and Hecla Strait and along the Melville Peninsula coast south to at least 68°N, remained heavily ice-bound until early September, thus for at least a month longer than in 1956. Similar year-to-year differences may occur in all parts of the basin and may be reflected, it is suggested, in the development of the plankton. First solid winter freezing of the surface begins usually between early October and early November, and the full winter state is reached at about the end of the calendar year. Most of the basin is covered by ice from 9 to more than 10 months per year.

THE ZOOPLANKTON

Zooplankton was obtained from both vertical and horizontal tows made with nets of No. 6 mesh (opening 0.239 mm), No. 0 mesh (opening 0.569 mm) and stramin (opening about 1 mm) on the M.V. *Calanus*, and with nets of No. 6 mesh only on the *Labrador*. Wet weights of vertical No. 6 net collections were computed by draining plankton on a fine filter over a vacuum flask and weighing on a balance sensitive to 0.005 g. Identifications and counts of organisms were made by examination of whole collections or, in the case of small organisms, of subsamples of various sizes, not less than 5%. For the purpose of comparison of standing crop in various parts of Foxe Basin, and of rough estimation of crop as compared to other geographical areas, counts of organisms and weights of samples are expressed as per cubic metre, on the basis of full straining efficiency of the No. 6 nets. This, of course, tends to give low values, and the tendency is extended by the inevitable escape of the faster moving species from vertically hauled nets. A number of species were taken in horizontal tows which were

made only from the M.V. *Calanus* in northern Foxe Basin, and suggest a greater relative specific composition for the northern area than a more equitable distribution of horizontal tows would have shown. These are included below in records of occurrence, but they are not used in quantitative estimates which are derived from vertical hauls only.

Weights of 45 collections are shown in Fig. 2, most of them taken from the upper 50 m. Of the stations where 50-metre collections were made, 17, between Fury and Hecla Strait and Foxe Channel and between Melville Peninsula and the eastern boundary of the southward flowing water (called subsequently the west side of the basin), showed a mean crop of 61 mg/m³ and a range of 32 to 108 mg/m³. Fifteen stations from the region of essentially northward water flow (called subsequently the east side of the basin) showed a mean crop of 29 mg/m³ and a range of 2 to 57 mg/m³. Of the collections made from 100 metres to the surface, three from the southwest part of Foxe Basin averaged 55 mg/m³, and three from west Foxe Channel 57 mg/m³. High values in central Fox Channel (93 mg/m³), indicating a larger population below than above 50 m in this region, may represent intruding plankters from the south, many of which do not extend any farther to the north. While the number of biomass measurements is small for application to a region of this size, the consistency of the data with respect to water movements and species occurrence indicate that the upper 50 m of the primarily arctic west side of Foxe Basin and Channel supports a zooplankton population (at least from July to October) of the order of twice the size of that found in the more mixed, generally shallower east side, and greater still than that found in the more or less bathymetrically isolated northeast corner of the basin. Deeper water in central Foxe Channel apparently brings from the south a larger population of zooplankton than occurs at the surface in this area, northward extension of this being largely limited to southernmost Foxe Basin, the bulk of it probably moving back to the south, for the most part in the deep water of west Foxe Channel.

Coelenterates

Eight species of hydromedusae and one scyphomedusa were collected. *Sarsia tubulosa* (M. Sars) was distributed generally over the area. Bell heights ranged from 3 to 11 mm, the smallest individuals occurring in July, the largest in late August and September. *Sarsia princeps* (Haeckel) was found only at M.V. *Calanus* station 723 (northwest), at 20 m. *Hybocodon prolifer* L. Agassiz occurred only at M.V. *Calanus* stations 804, 806 and 901 (northwest), between the surface and 50 m. Eight individuals were from 2 to 7 mm high, and included gravid, budding and immature medusae.

Bougainvillia superciliaris L. Agassiz occurred generally over the collection area. Heights ranged from 3 to 10 mm, and were slightly greater in August and September than in July. Most of the larger medusae, greater than 6 mm high, carried eggs from 8 August until at least late September. *Halitholus cirratus* Hartlaub was found over the whole of northern Foxe Basin. Heights were between 1 and 16 mm, and there was a clear indication of growth between July

and September. *Tiaropsis multicirrata* (M. Sars) was taken only at M.V. *Calanus* stations 712, 804 and 806 (west and northwest), the medusae from 4 to 11 mm in diameter. *Aglantha digitale* (O. F. Müller) was found widely over Foxe Basin and in Foxe Channel. Bell height varied from about 2 to 19 mm, and gonad length from about 1 to 7 mm. There was evidence of height increase between June and September, with the largest gonads appearing in August. Very young medusae were apparent only occasionally in August and September. In 50-metre water near shore at Igloolik (Grainger, 1959), young medusae were found from July until February, and no individual was taken at any time of the year with gonads more than 1.5 mm long. The majority of adults appear to exist, if not in deeper water, at least over deeper water than the 50 m found at Igloolik, and to be more numerous at offshore stations than close to shore. *Aeginopsis laurenti* Brandt was limited to M.V. *Calanus* stations 723, 803, 808, 818, 820 and 901, and only a few individuals were found. *Cyanea capillata* (L.) was taken generally over the northern part of Foxe Basin.

Ctenophores

Ctenophores were present in many collections, but because of their poor state of preservation only a few could be identified with reasonable certainty to species. *Mertensia ovum* (Fab.) was the more abundant among the identifiable specimens. Only a few *Beroë cucumis* Fab. were found.

Polychaetes

Three species of *Autolytus* occurred as a few specimens only. Larval polychaetes, of unidentified species, were common however, and were taken at many stations throughout Foxe Basin, often in large numbers. Only one *Autolytus prolifer* (O. F. Müller), a *sacconereis* with eggs, was taken, at M.V. *Calanus* station 804. *A. prismaticus* (Fab.) occurred at M.V. *Calanus* stations 715, 806, 828, 837 and 901. The 7 individuals found included 5 *sacconereis* and 2 *polybostrichus* forms. Two of the females (2 and 7 August) carried eggs. *A. alexandri* Malmgren occurred as only 4 *sacconereis* forms, all with eggs, found at M.V. *Calanus* stations 718, 824, 828 and 901.

Pteropods

The two common species of northern waters, *Clione limacina* (Phipps) and *Limacina helicina* (Phipps), were taken. *Limacina* (Fig. 3) was limited to the west side of Foxe Basin and the east part of Foxe Channel.

Chaetognaths

Sagitta elegans Verrill was the only species recorded. Distribution was general over the area investigated.

Copepods

Eight species of calanoids and two of cyclopoids were found, along with a few unidentified harpacticoids and monstrilloids. Occurrence of all species is shown in Tables I and II.

TABLE I. Qualitative (x) and quantitative (+, 1, etc.) occurrence of copepods of the *Labrador* collection. Numbers are of individuals per m³; + means fewer than 1 per m³.

1955

Station	70	71	72	73	74	76	119	124	125	127	129	131	133	135	144	149	153	155	157	158	165	168	173	175	177	179	185	187	189
Calanus glacialis	4	+	+	+	4	+	18	+	+	+	+	4	...	...	x	+	28	...	1	...	+	1	...	16	24	28	x	5	6
C. finmarchicus	+	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
C. hyperboreus	+	...	+	+	...	...	+	...	...	...	...	...	...	...	...	...	...	...	...	...	+	...	...	...	...	...	x	...	...
Pseudocalanus minutus	28	3	8	+	30	+	146	252	180	340	775	824	166	243	x	+	2272	x	332	x	+	188	342	224	298	312	...	104	168
Microcalanus pygmaeus	15	+	+	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	1	5	1	...	9	x	1	4
Gaidius tenuispinus	...	...	...	...	...	...	...	+	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
Metridia longa	2	+	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	13	10	7	...	...	...	...
Acartia longiremus	...	...	...	...	...	...	...	...	...	...	93	124	...	...	...	...	2229	x	1	x	...	1	...	1	2	1	...	...	...
Oithona similis	17	+	+	...	...	...	3	...	...	...	...	...	...	...	...	...	...	...	...	...	+	...	45	7	27	101	...	...	...
Oncaea borealis	3	+	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	1	...	13	...	...	5
Nauplii	10	...	7	+	30	+	13	23	36	33	95	131	45	91	x	+	129	x	1	x	+	8	75	18	40	85	x	4	1

1956

Station	41	43	44	48	50	51	52	58	66	68	77	84	86	90	92	98	99	101	104	118	122	123	124	125	126	130	131	132	134	141	143	144	145	146
C. glacialis	1	11	5	14	2	17	+	+	2	...	+	+	8	...	6	...	+	...	+	1	2	+	+	+	2	+	8	14	+	1	4	10	5	7
C. finmarchicus	...	3	+	+	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
C. hyperboreus	...	2	+	+	+	+	+	+	...	...	+	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	1	2	2	+
P. minutus	1	12	54	92	41	123	+	+	697	258	+	+	19	+	28	+	+	+	38	49	303	26	+	+	25	+	394	1536	86	160	226	88	55	37
M. pygmaeus	1	1	5	...	...	2	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	1	...	...
G. tenuispinus	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	+	...	...	...
M. longa	+	+	16	8	4	+	...	...	...	...	+	...	...	...	...	...	...	...	16	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...
A. longiremus	...	...	...	...	...	...	...	...	...	1	...	...	...	...	...	...	...	...	...	4	...	...	...	...	...	...	...	...	...	...	...	...	...	...
O. similis	1	6	23	11	...	9	+	...	...	...	+	+	5	...	15	+	+	+	12	...	...	...	+	...	...	+	...	...	...	1	10	3	8	17
O. borealis	...	...	3	1	2	...	...	...	...	...	...	...	1	...	6	...	...	+	...	...	...	...	...	...	+	+	...	...	...	...	...	2	4	...
Nauplii	...	26	97	10	7	83	+	+	328	190	+	+	197	5	262	+	+	+	48	1043	755	17	+	...	47	+	700	941	86	802	65	26	45	59

TABLE II. Qualitative (x) and quantitative (+, 1, etc.) occurrence of copepods of the *Calanus* collection. Numbers are of individuals per m³, + means fewer than 1 per m³.

Station	1955											1956																1957
	711	712	713	714	715	716	718	719	720	722	723	801	803	804	806	808	811	816	817	818	819	820	824	826	828	832	837	901
Calanus glacialis	x	x	21	x	20	x	x	x	50	26	x	x	x	+	x	x	+	x	x	x	x	x	2	2	x	...	x	x
C. hyperboreus	x	x	+	x	+	x	x	x	+	+	x	x	x	...	x	x	x	x	x	x	x	x	..	...	...	...	...	x
Limnocalanus macrurus	...	...	...	...	...	...	...	...	...	...	...	...	...	...	..	...	...	...	...	..	...	..	..	...	...	...	...	x
Pseudocalanus minutus	x	x	861	x	1345	x	x	x	858	169	x	x	x	268	x	x	x	x	x	x	x	x	524	614	x	x	x	x
Metridia longa	...	...	...	...	x	x	...	...	...	...	...	...	...	...	...	x	...	...	...	...	x	..	...	...	...	...	...	...
Acartia longiremus	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	x
Nauplii	x	x	x	x	60	x	x	x	10	3	x	x	x	5	x	x	x	x	x	x	x	x	48	14	x	x	x	x

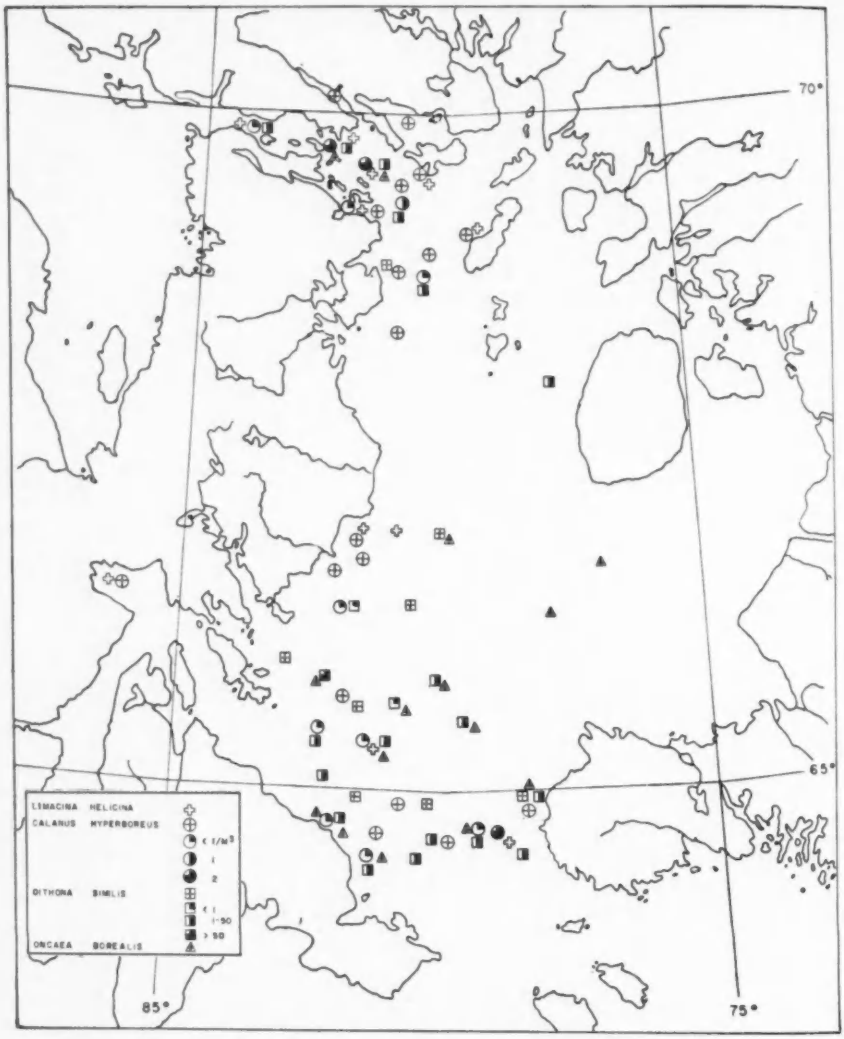

FIG. 3. Quantitative occurrence of four zooplankton species.

Calanus glacialis Jaschnov is the second most abundant calanoid in Foxe Basin, found over the entire area, but most numerously on the west side of the basin. Adult males were not found and adult females were limited almost entirely to July collections. *Calanus finmarchicus* (Gunnerus) was found only in south Foxe Basin and Foxe Channel (Fig. 4). Formerly recorded widely throughout circumpolar arctic and subarctic regions, the large northern representatives in the Old World were referred to the new species *C. glacialis* by Jaschnov (1955),

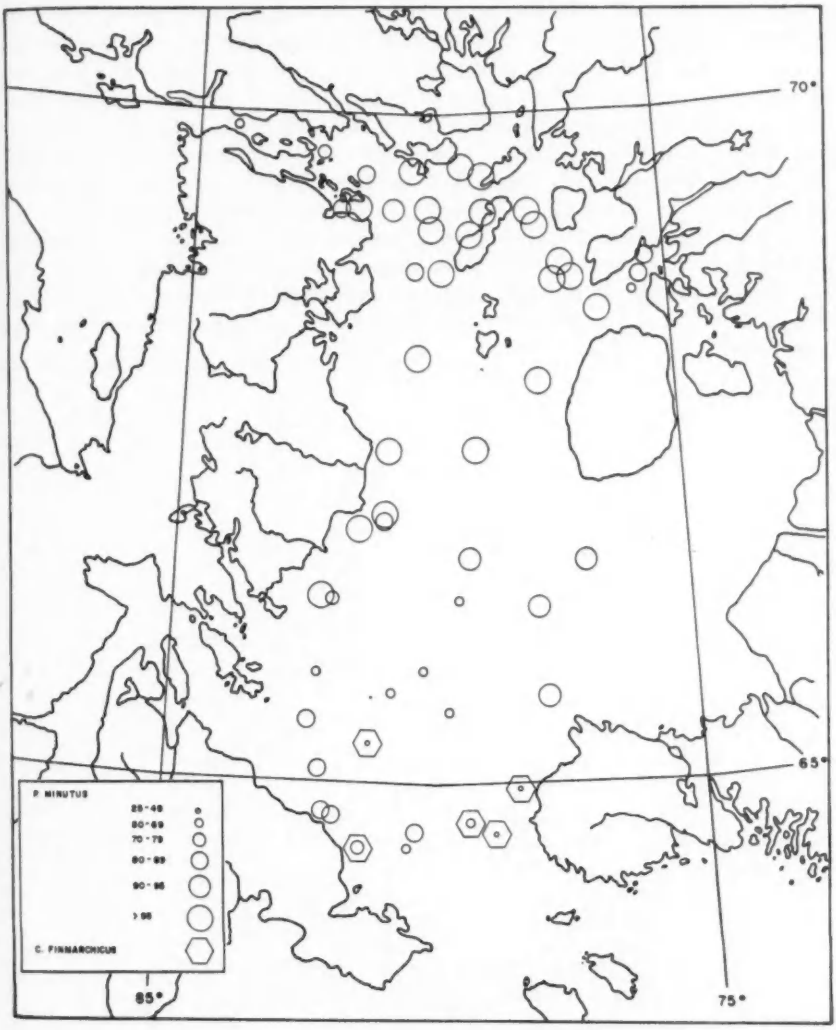

FIG. 4. Quantitative occurrence of *Pseudocalanus minutus* and qualitative occurrence of *Calanus finmarchicus*.

and only the small, essentially boreal members were retained in the species *finmarchicus*. Recently a similar situation was reported in North American *Calanus* by Grainger (1961); *C. glacialis* is the arctic form, and *glacialis* and *finmarchicus* together are characteristic of subarctic waters.

Calanus hyperboreus Krøyer occurrence is shown in Fig. 3, where distribution is seen to be distinctly limited to the west side of Foxe Basin, but to extend

across Foxe Channel. Numbers were small, never exceeding 2 per m^3. Adult females occurred in most collections, and none younger than stage III was found.

More than 400 individuals of *Limnocalanus macrurus* Sars, a freshwater species, were found on two occasions in surface water of low salinity (less than 2‰) at M.V. *Calanus* station 901. These copepods were presumably derived from a lake (where the species was known to occur) which drains into Frustration Bay, Rowley Island. They were able to exist in the upper, brackish layer which was being nurtured by melting ice, several miles from the river mouth.

Pseudocalanus minutus (Krøyer) occurred at nearly all stations, and appeared to be the dominant calanoid in Foxe Basin. Occurrence is shown in Fig. 4, expressed as percentage of the total number of copepods at each station. It was never found as less than 25% of total copepods, and at a few stations it was the

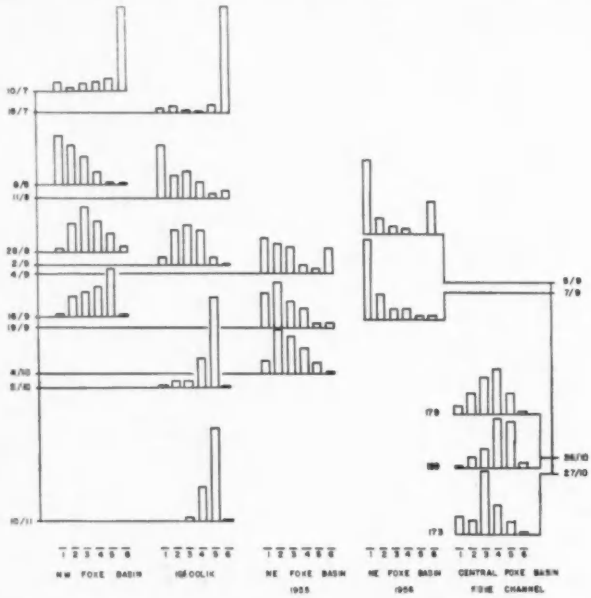

FIG. 5. Relative occurrence of copepodite stages of *Pseudocalanus minutus*. Explanation in text.

only copepod collected. It is seen (Fig. 4) to be strongly dominant (to 95% or higher) south to about the latitude of Frozen Strait, and to become relatively less abundant farther south, the lowest values (frequently less than 70%) occurring in south central Foxe Basin and east Foxe Channel. Coincidence between the area of southern reduction in *P. minutus* and the northern limit of *Calanus finmarchicus* is marked (Fig. 4).

The development rate of copepodite stages of *P. minutus* shows fairly consistent variations in different areas of Foxe Basin (Fig. 5). The left column of histograms shows percentages of copepodite stages I to VI ♀ between July 10

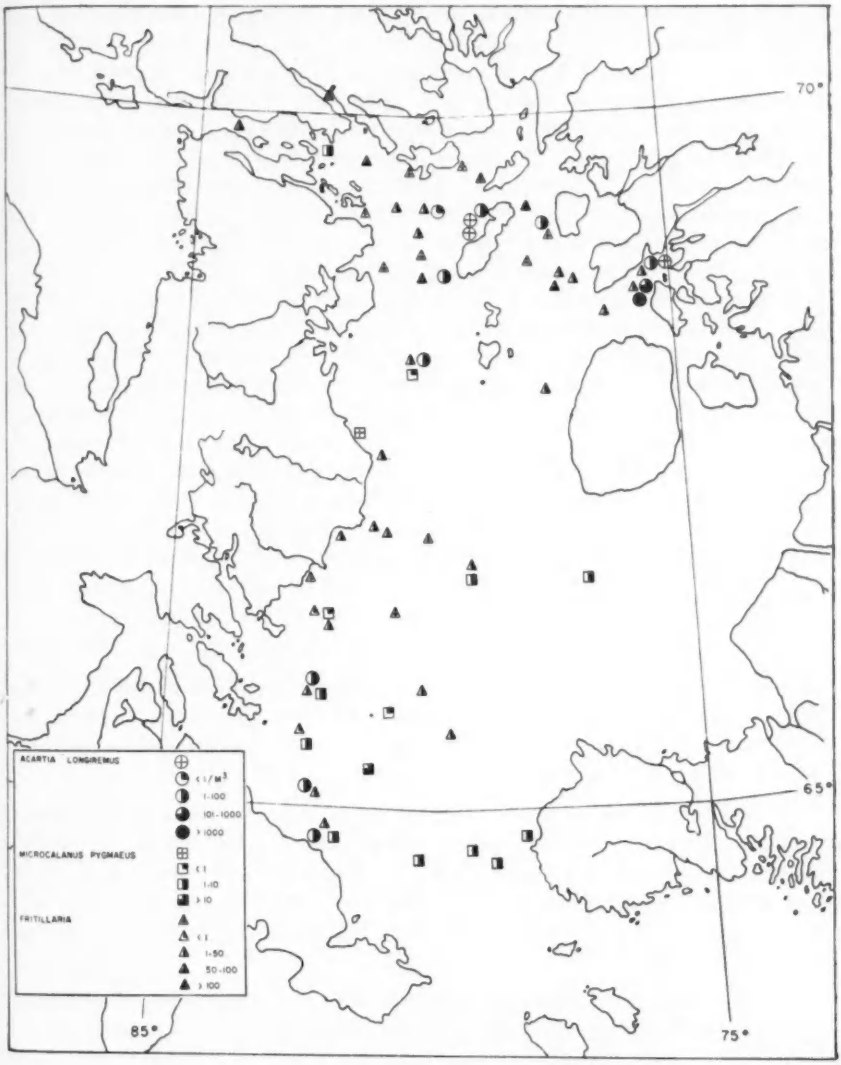

FIG. 6. Quantitative occurrence of three zooplankton species.

and 16 September at 4 stations in northwest Foxe Basin. Beginning with dominance of adult females (10/7), successive dominance of stages I (8/8), III (28/8) and V (16/9) appear. The second column shows development at Igloolik between 15 July and 10 November (from Grainger, 1959). There is close agreement between the two sets of data during the common time period, with development at Igloolik showing increased numbers of stage V and eventual dis-

appearance of stages I and II in October and November. In the third and fourth columns are shown development in northeast Foxe Basin in 1955 and 1956. In 1955, stage I was still strongest and adult females numerous on 4 September, and stage II was the most abundant on 4 October, while at approximately the same times of the year stages III to V were most numerous in the northwest area. In 1956, still later development is suggested, with stage I strongly dominant on 7 September. Thus in both 1955 and 1956, and evidently to a greater degree in 1956 than in 1955, development in the northeast was considerably later, of the order of 2 or more weeks, than in the northwest. In the fifth column of Fig. 5, development at *Labrador* stations 179 and 189 (1955, south central Foxe Basin) and 173 (1955, Foxe Channel) shows dominance of stage IV in Foxe Basin and stage III in Foxe Channel on 26 and 27 October. As these compare with the condition found in northwest Foxe Basin in late August and early September, there appears to be in the southern part of the area studied extreme retardation of up to 8 weeks. The reasons for variations in development rate are not entirely clear, although later development appears to be related to the apparent generally lower secondary production in the east and south central areas than in the northwest and west sections of Foxe Basin. Year-to-year variation may in some instances be related to differences in the duration of ice cover which, for example, persisted longer over the northeast sector in 1956 than in 1955, and may therefore have delayed the onset of summer primary and consequently secondary production in 1956 to a later date than in 1955.

Microcalanus pygmaeus G. O. Sars was one of the rarest copepods, found most often in Foxe Channel and south Foxe Basin, and in smaller numbers in the north section (Fig. 6). A species known to occur near the surface in the Arctic Ocean and in deeper water towards the south, its distribution in Foxe Basin coincides with the deeper stations.

Metridia longa (Lubbeck) was taken almost exclusively at the deeper stations, sparsely in the northwest area, more numerously in southwest Foxe Basin and most abundantly in Foxe Channel (Fig. 7). Both male and female adults were taken over the full time range of the collections. No member of stage I was found, and stages II and III were taken only in late October at *Labrador* station 173 (Foxe Channel).

Acartia longiremus (Lilljeborg) was collected most abundantly in the region between Baird Peninsula and Prince Charles Island, also west to Rowley Island and in the southwest part of the basin (Fig. 6). Numbers were small (not more than 2/m^3) everywhere except at *Labrador* station 153 (1955) where the enormous concentration of 2,229/m^3 was recorded and at stations 129 and 131 (1955) where large populations also were found. During the period between first and last occupations of these 3 stations (5 September to 4 October) adult females declined from 40 to fewer than 1/m^3, and dominance passed successively from stage I to stage III. There is little known yet of the biology of *A. longiremus* in northern waters. Fontaine (1955) found adults dominant in June and early July, copepodite stages I and II between August 11 and 19 in Ungava Bay. Development

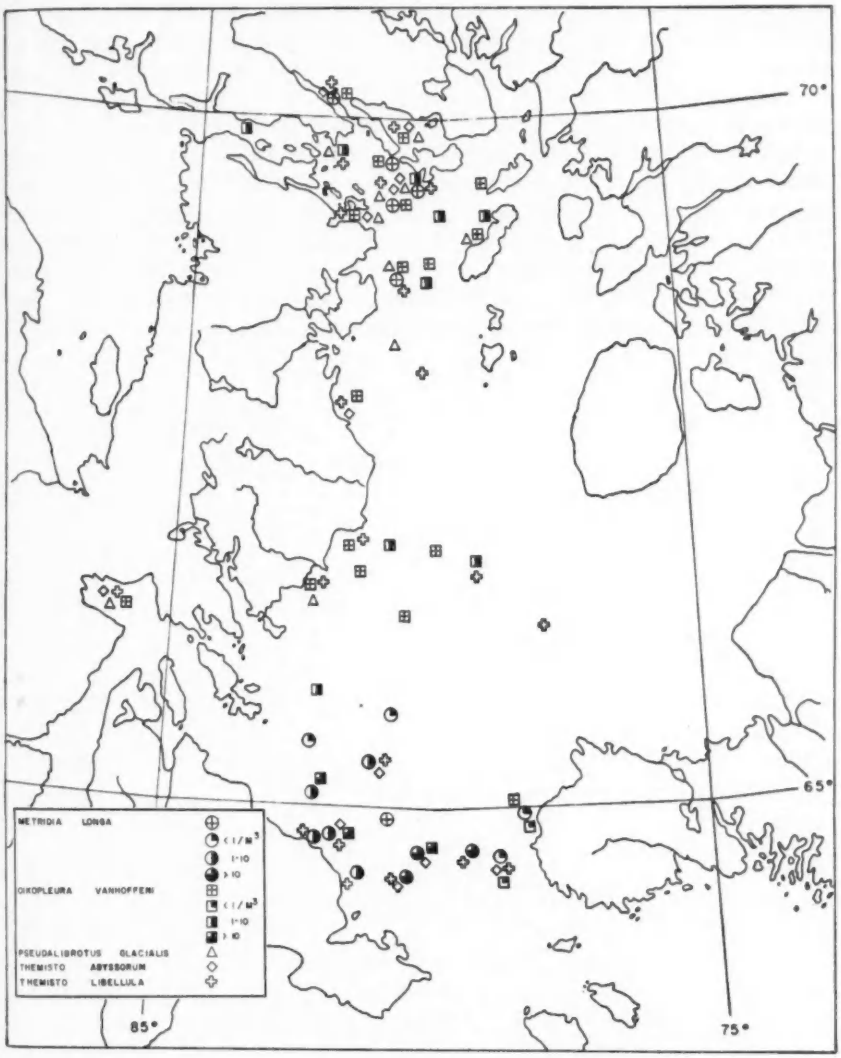

FIG. 7. Quantitative occurrence of five zooplankton species.

in Foxe Basin is evidently delayed long after that time, at least in the northeast region.

Two males which appeared to be intermediate to stages V and VI were found. Fig. 8 shows the fifth legs of a typical stage V male, with the same legs of a typical stage VI male. In Fig. 8b however is shown a pair of fifth legs which obviously fit into neither stage V nor VI, although the possession of only

4 urosome segments would tend to place the individual in stage V. Of special interest here is the close agreement between the fifth legs of this intermediate specimen and Grandori's (1912, plate X, fig. 207) illustration of the fifth legs of a European specimen of *A. clausi*. Grandori, in an attempt to define the developmental stages of *Acartia*, proposed more than the now accepted 6 copepodite stages, one being this apparently intermediate form. Occurrence of such closely similar abnormalities, if indeed that is what they are, in such widely separated places in two species of *Acartia* suggest that this form may occur more often than reported to date. All specimens examined for the structure showed on the second segment of the left fifth leg of adult males an internal seta, used by Pinhey (1926, fig. 5) to characterize *A. longiremus spiniremus*. Fontaine (1955) found that all individuals examined for it showed the same structure in Ungava Bay.

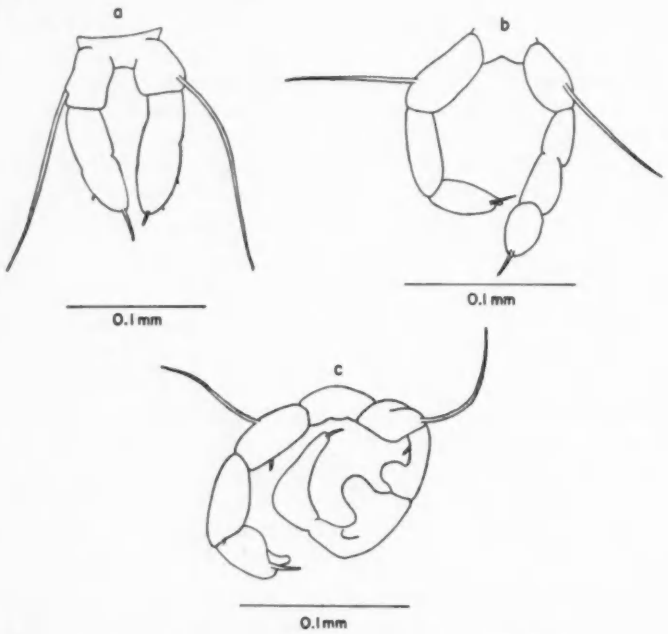

FIG. 8. Fifth legs of *Acartia longiremus*. (a) Stage V male, typical form, (b) stage V male, intermediate form, (c) stage VI male, typical form.

Oithona similis Claus was widely distributed, except in the northeast region (Fig. 3). Adult females dominated in most July and August collections, stage I appearing at the end of July. Stage II was most numerous after mid-September, stage V during the second half of October.

Oncaea borealis G. O. Sars showed wide distribution of relatively few individuals (Fig. 3).

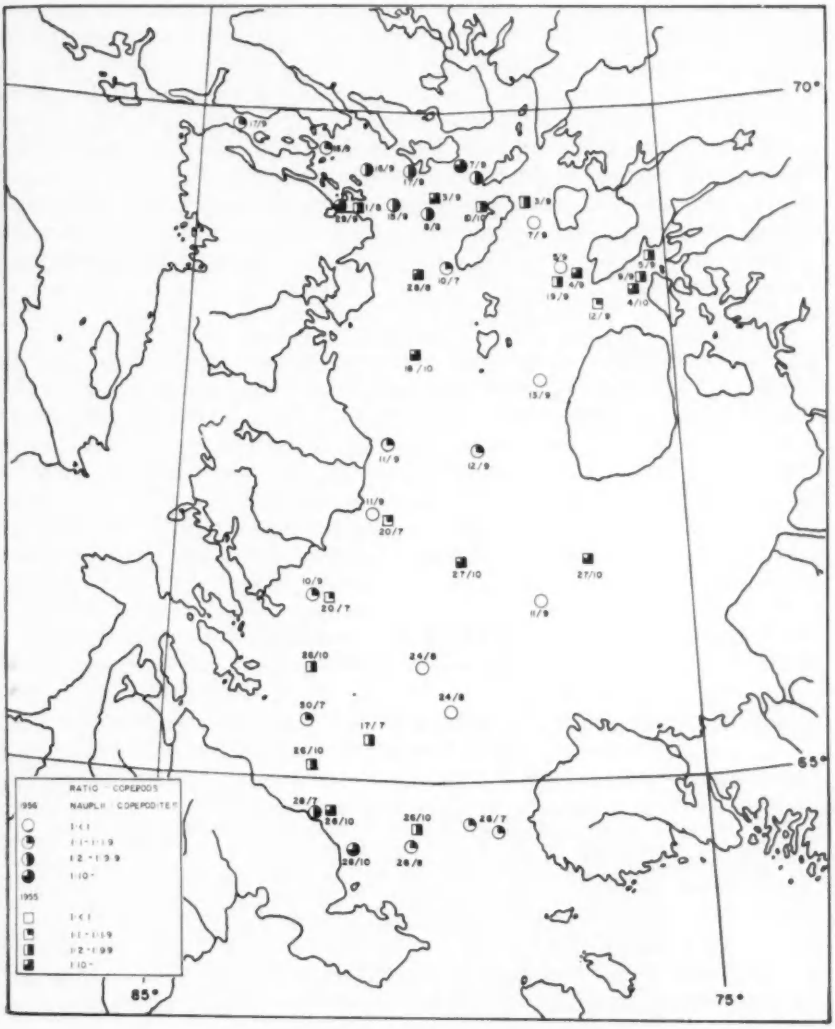

FIG. 9. Ratio of copepod nauplii to copepodites.

Nauplii of copepods were taken at nearly every M. V. *Calanus* and *Labrador* station, and numbers varied from more than 1,000 to fewer than 1 per m^3. Fig. 9 shows ratio of copepod nauplii to copepodites (all species). In general, and as was to be expected, the ratio was found to decrease through the seasons, the smallest relative number of nauplii being found in late autumn. This sequence however is noticeably more regular in the 1955 than in the 1956 material, espe-

cially in the southern and northeastern areas. Four 1956 stations in south Foxe Basin (two on August 24, two on September 11) showed more nauplii than copepodites, while at the nearest 1955 stations nauplii had declined and copepodites were more numerous at about the same time of the year. In the northeast sector, a difference between the two years is shown again. The 1955 stations in early September supported more than twice as many copepodiites as nauplii, while the 1956 stations produced more nauplii than copepodites at the same time of the year. These observations are in accordance with *Pseudocalanus* data (above) in illustrating delayed development in 1956 over 1955, and in showing variations in the time of nauplii development in different parts of the basin within single years.

AMPHIPODS

Twelve amphipod species were collected. *Pseudalibrotus glacialis* G. O. Sars was limited to the northwest and west regions and was found too in Repulse Bay (Fig. 7). Individual lengths were from 4 to 14 mm, and in the larger collections two distinct size groups were present during most of the collecting period. Females from about 10 to 14 mm, carrying eggs, were found between 6 August and 10 October. *P. nanseni* G. O. Sars was collected from Fury and Hecla Strait south to near Frozen Strait. Specimens varied in length from 7 to 17 mm. None of the females carried eggs. *Apherusa glacialis* (H. J. Hansen) was found in northwest Foxe Basin only. *Gammarellus homari* (Fab.) occurred as a single individual only, 6 mm long, in the northwest area. *Gammarus wilkitzki* Birula appears to be the dominant planktonic gammarid, found over most of the basin. *Gammaracanthus loricatus* (Sabine) was found at 4 stations only, all in northwest Foxe Basin.

Hyperoche medusarum (Krøyer) was limited in collections to the north and central areas. Only young individuals were found during July (2–4 mm) and during the first half of August (3–6 mm). The first adult male (8 mm) was taken on 26 August, the last immature specimen on 28 August. Adult males remained in the plankton until at least 17 October, while females with eggs appeared first on 29 September and also remained until at least 17 October. These data, along with those of the author from Igloolik (Grainger, 1959) shows in north Foxe Basin only young specimens (1.6–4 mm) from February to July, slightly larger individuals (3–6 mm) in early August, adult males from the end of August and gravid females from the end of September until at least late October. *Hyperia medusarum* (Müller) was rare in west Foxe Basin. Most were immature, about 4 mm long, and there was one adolescent male of 6.5 mm, the latter taken on 26 August. *Hyperia galba* (Montague), found in the west only, consisted of individuals from 7.5 to 20 mm long, including mostly immatures, adolescent and adult males and a single non-ovigerous female. Only young specimens of *Themisto abyssorum* (Boeck) were collected, all in the western area (Fig. 7). *Themisto libellula* (Mandt) occurred widely over the west side of the basin (Fig. 7), only immature individuals being taken. Two specimens of *Themisto gaudichaudi* (Guérin) were found, one in northwest Foxe Basin and one in Foxe Channel. Both were immature.

Cirripeds

These occurred over most of the area investigated. Numbers of nauplii varied from none to more than 1,000/m³, of cypris larvae from none to 32/m³. The greatest proportion of cypris larvae occurred generally in the northwest and west regions, the lowest in the east.

Mysids

Only a few specimens of *Mysis oculata* (Fab.), from 6 to 26 mm long, were collected. None of the females bore eggs and only the largest (26 mm) displayed a conspicuous marsupium.

Cumaceans

Five individuals of *Lamprops fuscata* G. O. Sars were collected at M. V. *Calanus* station 901 (Rowley Island) in the upper 10 m. on 6 August. This is the first record of the species from the Canadian arctic-subarctic region north of Newfoundland. Further distribution includes West Greenland, north Norway, Novaya Zemlya, Franz Joseph Land (Stephensen, 1913), Spitzbergen (Stephensen, 1943), Barents Sea (Jaschnov, 1948), Newfoundland and south Alaska (Calman, 1912), from which it would appear to be primarily a subarctic species. The 5 individuals collected were all females, between 4 and 5 mm total length. Four carried eggs about 0.4 mm in diameter.

Euphausids

Five specimens of *Thysanoessa inermis* (Krøyer) were taken, all of them immature males of 24 to 27 mm total length, at M. V. *Calanus* stations 711, 808 and 820 and *Labrador* station 177 (1955). *T. raschi* (M. Sars) was found only at M. V. *Calanus* station 711 and *Labrador* stations 173 (1955) and 177 (1955), in Foxe Channel, southwest Foxe Basin and Repulse Bay.

Decapod Crustaceans

Nearly all the decapods taken in the plankton were larval forms, and occurred widely over the whole collection area. Most were hippolytids, reaching a maximum length of about 15 mm. Some were *Eupagurus* sp., between 6 and 7 mm long. Six individuals of *Eualus gaimardi* (Milne Edwards) were found at M. V. *Calanus* stations 714 and 901, and were from 36 to 45 mm long.

Tunicates

Oikopleura vanhoeffeni Lohman occurred along the west side of the basin, in Foxe Channel and Repulse Bay (Fig. 7). Occurrence of *Fritillaria borealis* Lohman (Fig. 6) was widespread over the northern part of the basin and along the west side. It was not found in Foxe Channel. Tunicate larvae were taken at 10 *Labrador* stations.

DISCUSSION

While detailed knowledge of zooplankton distribution in northernmost North America is still meagre, it is possible, using known distribution data on some of the species, to speculate on the origin of water masses in Foxe Basin from

the occurrence of the zooplankton. For this purpose two groups of plankton may be distinguished, one serving to indicate arctic water, the other mixed Atlantic-arctic (subarctic) water, to show the extent of influence of arctic waters entering the basin from the north, and of the subarctic element introduced from the south. None of the species may be said to belong exclusively to either the arctic or subarctic waters, and in fact the majority of species show little value at all as indicators of either of these water masses, occurring as they do in apparently more or less equal numbers through both regions. A few species however appear to be more successful, developing larger populations and occupying relatively more important positions among the plankton, in one region than in the other. Relative occurrence therefore, rather than simple presence in one area and absence from another, is the criterion used for the most part here in distinguishing indicators of the two water masses.

Among the arctic water indicators are the medusa *Aeginopsis laurenti*, the copepods *Calanus glacialis*, *C. hyperboreus*, *Microcalanus pygmaeus*, *Pseudocalanus minutus*, and the amphipods *Pseudalibrotus nanseni*, *Apherusa glacialis*, *Gammarus wilkitzki* and *Themisto libellula*. Of these, *C. glacialis* occurring without *C. finmarchicus* appears to be the most useful true arctic indicator. The remaining species, excepting *G. wilkitzki* and *T. libellula*, are known from surface and deep waters of the Arctic Ocean (Sars, 1900; Bogorov, 1946; Brodsky and Nitikin, 1955; Mohr, 1959), and occur in their greatest numbers in the upper, colder waters of the northernmost regions, tending to appear in smaller numbers in the deeper, colder waters to the south. In Foxe Basin, *C. glacialis* (without *C. finmarchicus*) was found predominantly on the west side, south to Foxe channel, *C. hyperboreus* on the west side only, as well as across Foxe Channel, *P. minutus* in greatest numbers in the north and central regions, conspicuously less numerous in the south and in Foxe Channel, the remaining species primarily in the north and west.

Included among the subarctic indicators are the amphipods *Hyperia medusarum* and *Themisto abyssorum* and the copepod *Acartia longiremus*, all of which are known as well from the Arctic Ocean, the first two at least primarily from deep rather than surface waters. The other subarctic species, the medusae *Tiaropsis multicirrata* and *Hybocodon prolifer*, the amphipods *Hyperia galba* and *Themisto gaudichaudi*, are rare in arctic regions. *Calanus finmarchicus* appears to be the best indicator of subarctic and boreal waters. Apart from the 3 species recorded from the Arctic Ocean, the others given here are not known from farther into the arctic area (in North America) than the Foxe Basin localities given here. One of the species requires special comment. The medusa *Hybocodon prolifer* was long considered as northern boreal and not as an inhabitant of arctic waters (Kramp and Damas, 1925; Kramp, 1926). Specimens reported as probably being of this species were taken in large numbers however by Dunbar (1942) during July and August at Lake Harbour, north central Hudson Strait. In the same year (Kramp, 1942), it was reported for the first time from West Greenland, from as far north as Disko Bay. Dunbar (1951) used the Lake Harbour record to interpret westward extension of subarctic water at least as

far as Lake Harbour along the north side of Hudson Strait. Following recent work on the medusae of the M. V. *Calanus* collections, *H. prolifer* has been found to extend westward as far as Hudson Bay (personal communication from Miss Barbara Barry), and from the records here to extend in small numbers to northern Foxe Basin. It therefore appears to be a mixed-water rather than an exclusively boreal species.

From the data on occurrence of plankton species, Foxe Basin appears to enclose the boundary, in this part of Canada, between the southernmost limit of arctic and the northernmost extent of subarctic water. The dominant element within the basin appears to be the arctic one, introduced from the north through Fury and Hecla Strait and shown most distinctly in the western section of Foxe Basin and to a lesser degree in west Foxe Channel. The opposing subarctic element, entering from the south through central to east Foxe Channel, appears to be confined largely to south Foxe Basin. A few species indicating subarctic influence however occur in small numbers as far north as the northern part of the basin. This very minor subarctic element may reach the north of the basin via the shallow waters of the east side.

It is reasonable to expect neither precise nor constant lines of demarcation between regions of fully arctic and subarctic character, and that irregular as well as annual fluctuations may occur. As Ellis (1960) pointed out, seasonal similarities between arctic and subarctic areas may develop in summer in the upper water layers as a result of increased insolation. Parts of Foxe Basin show a comparatively slight but significant summer warming of the surface waters to more than O°C, and it is possible that this may bring about a temporary change in vertical distribution of some of the cold-water species in summer. This may be at least partly responsible for the rarity of such species as *Calanus hyperboreus* (demonstrated as being many times more abundant below than above 50 m. in north Foxe Basin in August) and *Microcalanus pygmaeus* in shallow waters during the summer season. Stations where they occurred are almost exclusively in deep water. This suggests that short-term, *in situ* changes may take place in true arctic water, resulting in conditions resembling those of the subarctic, and that temporary faunistic changes may accompany them.

The apparent sharp division in quantity and quality of zooplankton between the western and eastern parts of Foxe Basin is a conspicuous feature of the area. It may be explained in part by the character of plankton carried in opposing water masses moving into the basin from the north and south and by differences in depth between the two halves of the basin, the latter especially influencing the occurrence of normally deep-water species. Another factor of probable consequence here is seasonal differences in various parts of the basin, associated in part with differences in duration of ice cover. Turbidity of the shallow water of east Foxe Basin may exert an inhibiting influence on plankton development in that area. Campbell and Collin (1958), in a discussion of the problem of the origin of the characteristically discoloured Foxe Basin ice, suggested that fine bottom sediments in areas below shallow water (a condition especially characteristic of the east side of the basin) are forced into suspension by wind-activated

water movements, and that high degrees of turbidity are thus brought about. The authors proposed that near-shore development of turbidity is followed by gradual offshore movement of the "muddy water". While the extent of such development and subsequent spread of turbid water is not known, it would appear that the most intense turbidity would be established over the large expanse of shallow water in east Foxe Basin, and that quantity of suspended matter within the water would diminish with increasing distance away from the area.

Thus water movements, depth distribution, ice cover duration and turbidity are suggested as the main environmental factors influencing the occurrence of zooplankton species in Foxe Basin, resulting in both a quantitatively and qualitatively richer plankton in the west than in the east part of the basin. It may appear anomalous for the arctic area of Foxe Basin to support a greater quantity of zooplankton than the partly mixed water of the east side, because subarctic waters characteristically produce greater zooplankton volumes than arctic waters. This must be attributed here to inhibiting factors, primarily turbid and shallow waters, found in the eastern area. Delayed secondary production in the east is shown by the recording of the largest standing crops in that area in late September and early October. In the west however, the largest zooplankton volumes were found generally in late August and September, and diminished quantities were taken on later dates. Secondary production appears to have been both lower and later in the east, delayed during the short summer season, then cut short by the onset of winter conditions following an extremely short summer period.

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The Occurrence of the King Crab, *Paralithodes camtschatica* (Tilesius), and of *Lithodes aequispina* Benedict in British Columbia[1]

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ABSTRACT

Locality records are given of the capture of a number of king crabs in British Columbia waters. The extension of the known range of *Lithodes aequispina* to southern British Columbia is also reported. As these two species can be easily confused, figures and anatomical comparisons are provided.

INTRODUCTION

According to Marukawa (1933) and Makarov (1938), *Paralithodes camtschatica* (Tilesius), commonly known as the king crab, has been found northward from the Sea of Japan, eastward to the Bering Sea, southward into Alaskan waters (Benedict, 1894) and at Skidegate, Queen Charlotte Islands, British Columbia (Rathbun, 1919). In 1930 a specimen was collected west of the Queen Charlotte Islands (Newcombe, 1932), and since this time other specimens have been captured and are recorded here.

The published range of a closely related species, *Lithodes aequispina* Benedict, is Japan, Okhotsk and Bering Seas (Benedict, 1894; Makarov, 1938). The capture of this species in southern British Columbia waters is, therefore, a considerable extension of the known range and a first record for Canada.

These two species of crabs are sufficiently alike to be easily confused and thus we include figures of both species and some comparisons of the anatomy. In addition to this, some details of the life history of *Paralithodes camtschatica* are given.

ANATOMY AND TAXONOMY

Both these crabs belong to the family Lithodidae, tribe Anomura. These lithodid crustacea are crab-like, but due to their probable descent from hermit-crab ancestors, they differ in a number of respects from the true crabs. The exoskeleton is often very spiny, and although they do have five pairs of pereiopods or walking legs, the first pair are unequal in size and the fifth pair are much

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smaller than the others. The latter are not used for walking but are kept hidden under the back of the carapace and used only for cleaning the shell or for transferring sperm. Another distinguishing character of this group is that the antennae are external to the eyes, instead of internal, as in the true crabs.

The genera *Paralithodes* and *Lithodes* differ mainly in the calcification of the plates of the second segment of the abdomen. In the former, the outer part of the segment is composed of five distinct plates separated by evident sutures, while in the latter these plates are more or less fused, showing fairly definite separation of the outermost plates and only slight or no separation of inner plates (Fig. 1 and 2).

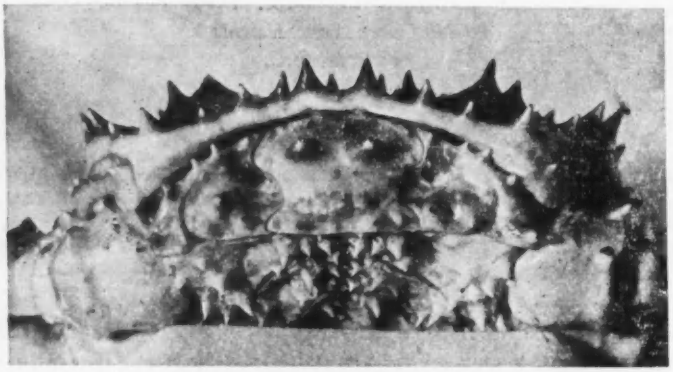

FIG. 1. P. *camtschatica*, posterior view to show second abdominal segment.

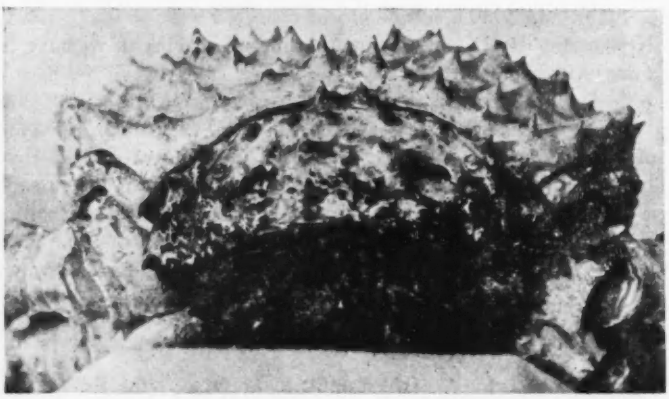

FIG. 2. *L. aequispina*, posterior view to show second abdominal segment.

Paralithodes camtschatica (Tilesius), Fig. 3, is well armed with large sharp spines. These vary considerably in size and shape according to the size and perhaps the sex of the individual. Thus a small specimen looks much more spiny

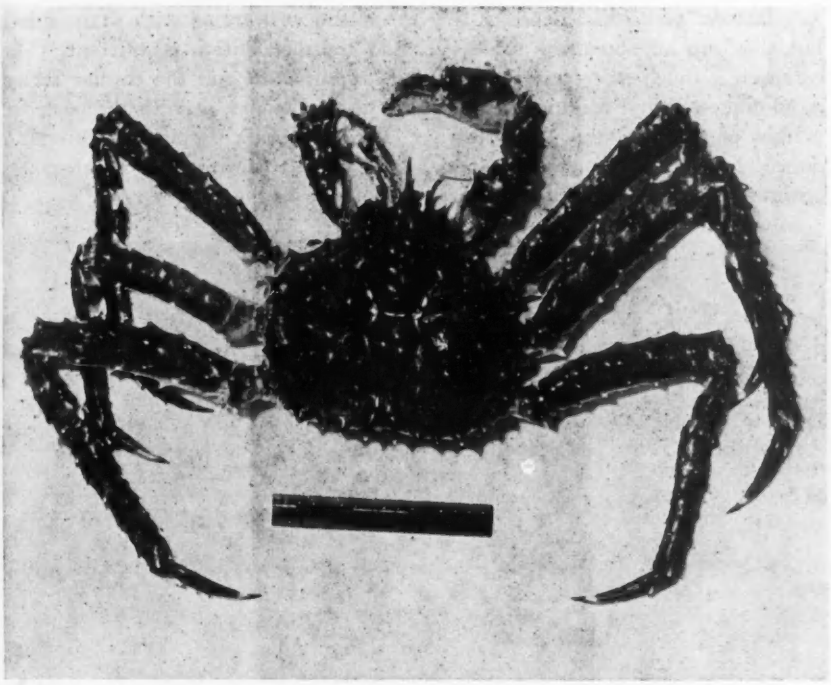

FIG. 3. *P. camtschatica*, dorsal view; male from Kitkatla Inlet.

than a large adult, but the number and location of the spines show little variation. There are six strong spines on the cardiac region of the carapace, and only one on the exopod or scale of the antenna. These two characters appear to distinguish this species from allied species found within the same range. A pair of dorsal spines is present on the rostrum, above the base of the eyestalks; a medial dorsal spine (which may be bifid) is anterior to these and terminates in a sharp curved spine (Fig. 4A).

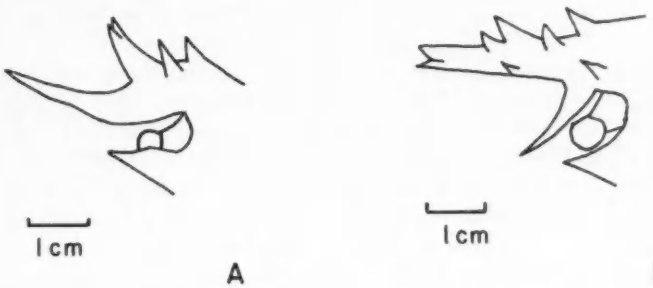

FIG. 4 A. Lateral view of rostrum of *P. camtschatica*. B. Lateral view of rostrum of *L. aequispina*.

Lithodes aequispina Benedict (Fig. 5) is also well armed with sharp spines but they are all about the same size, and the distribution is different. The carapace is much more convex than in *P. camtschatica* and the cardiac region more depressed and continuous with the intestinal region, or with the posterior margin of the carapace. The rostrum (Fig. 4B) bears 9 spines: 4 lateral, 2 dorsal, 2 terminal (bifurcate tip) and 1 large curved ventral spine which points downwards. There are 2 or 3 spines on the scale of the antenna.

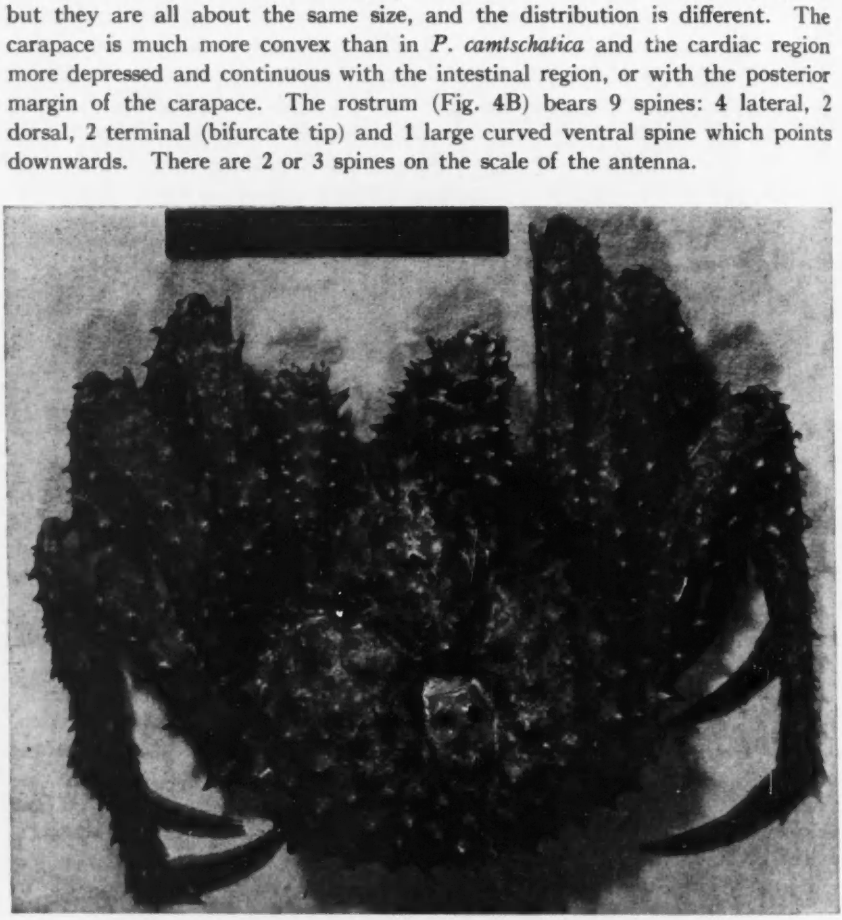

FIG. 5. *L. aequispina*, dorsal view; male from Queen Charlotte Sound.

Orginally the genus *Lithodes* comprised all the species now known as *Paralithodes* as well as *Lithodes*. The king crab is, therefore, listed in early records as *Lithodes camtschatica*. In the eastern and western North Pacific region only three species of *Paralithodes* are known: *P. camtschatica* (Tilesius), *P. platypus* Brandt and *P. brevipes* Milne-Edwards and Lucas. *P. rathbuni* (Benedict) and *P. californiensis* (Benedict) have been taken in deep water in California (Goodwin, 1952). A number of species of *Lithodes* have been described, but apparently only *L. aequispina* Benedict and *L couesi* Benedict are from the eastern North Pacific area.

LIFE HISTORY OF *PARALITHODES CAMTSCHATICA*

The following short summary has been adapted from Marukawa (1933). King crabs mature at a carapace width of 100 or 110 mm, at an estimated age of about 10 years. In the spring, they migrate from the winter habitat in deep water (115–200 fathoms, 210–366 m) to shallow, inshore water, the females preceding the males. The breeding pairs participate in an unusual kind of courtship activity of "hand-shaking", which may continue as long as a week. Moulting of the female precedes extrusion of the eggs and their fertilization. The developing eggs are retained on the abdomen of the female for about a year after which they hatch into free-swimming larvae. Larval development requires from seven to twelve weeks, depending upon water temperature, and there are four zoeal stages and one post-larval stage.

Marukawa's tagging experiments showed that king crabs migrate extensively. The maximum distance travelled by a tagged crab was 300 nautical miles (556 km) in 290 days. Males showed a maximum rate of migration of about 7.1 miles per day and females 5.6 miles per day (13.1 and 10.4 km/day). In addition to the seasonal breeding migration mentioned above, the crabs make further migrations in search of food during the summer.

OCCURRENCE OF *PARALITHODES CAMTSCHATICA* IN BRITISH COLUMBIA

Captures of king crabs in British Columbia are listed in Table I.

The five specimens caught in Prince Rupert Harbour in 1930 were originally described as the new species *P. rostrofalcatus* by MacKay (1932). We do not think they represent a valid species, but actually are the young of *P. camtschatica* (Tilesius). Dr Waldo L. Schmitt has examined some of these specimens and concurs with this opinion. MacKay distinguished these crabs mainly because

TABLE I. Records of king crab, *Paralithodes camtschatica* (Tilesius) from British Columbia.

Date	Locality	Depth	Sex	Carapace		Vessel or collector	Remarks
				Width	Length		
		m		mm	mm		
1930	West coast Queen Charlotte Islands	...	♀	163	152+	P. H. Johnson	Rostrum broken
Early 1940's	Captain Cove	24	..	(90 cm between tips of legs)		Lighthouse tender *Bernie*	Newspaper cut and report
Oct. 1930	Prince Rupert Harbour	27	♂ ♀	87 96	108 84	D. C. G. MacKay	
Autumn, 1956	Boundary Bay	...	..	(46 cm between tips of legs)		Commercial trawler	Died by accident, December 31, 1956
Feb. 2, 1960	Kitkatla Inlet	44–51	♀	153	140	J. A. Thomson	Ovigerous
July 31, 1960	Kitkatla Inlet	shore	..	...	...	T. H. Butler	Remains of cast-off shells
Nov. 28, 1960	Baker Inlet	37–46	..	...	...	*Strafen*	Identification verified, but specimen not obtained
Feb. 13, 1961	Kitkatla Inlet	12 and 27–42	4 ♂ 1 ♀	123–164 152	108–141 131	P. G. Squarebriggs	Also remains of 6 cast-off exoskeletons

of the long rostrum and spines, but other authors all state that spines of young specimens are well developed and become blunt with increasing size. The specimens we have examined exhibit these characteristics.

More recently three living king crabs were taken in the vicinity of Bellingham, Washington, some time before February 2, 1956 (Report in The Fishermen's News of this date), and one in Boundary Bay, British Columbia, in the fall of 1956, which lived for several months in the Vancouver Public Aquarium, Vancouver, British Columbia. The place of capture of these specimens is probably not within the normal range. In November, 1954, a number of king crabs brought to Bellingham in live boxes from the Bering Sea were considered to be dead and thrown off the dock, and also during 1955 living ovigerous females were kept in tanks at Anacortes, Washington, by Dr E. Chin, then of the United States Fish and Wildlife Service. We think it probable that one of these introductions was the source of the Bellingham and Boundary Bay specimens.

On February 2, 1960, an ovigerous female was caught in Kitkatla Inlet by the crew of the *A. P. Knight*, a research trawler of the Fisheries Research Board of Canada. On February 13, 1960, Captain C. Watson and Mate R. A. Dean of this ship were on the beach bordering this locality and reported seeing many cast-off exoskeletons of king crabs, but no specimens were collected. On July 30, 1960, trawl tows and a tangle net set in the same area by the *Investigator No. I* (also a Fisheries Research Board vessel) failed to catch any king crabs. The following day a search on a stretch of beach about half a mile long produced weathered remains of two carapaces and about 15 pereiopods lying along the highest line of drift. Presumably, these fragments were part of the litter of shells seen on the beach earlier in the year.

On February 13, 1961, when the *A. P. Knight* again visited the same area, P. G. Squarebriggs, the engineer, collected four crabs and shells while skindiving at a depth of 40 feet (12 m). He reported that the bottom was composed of sand and rocks with kelp attached and that there were live crabs and cast shells together. On the same day another specimen was taken in the trawl at 15–23 fathoms (27–42 m). The bottom water temperature was 9.2°C on July 30, and 5.8° on February 13.

Thus, there is evidence that king crabs inhabit Kitkatla Inlet during late winter, presumably during the breeding season, but are absent during the summer. As they are known to be cold-water animals, it is probable that they migrate to deeper water when temperatures rise in the spring. The region adjoining, Ogden Channel (Fig. 6), which has a considerable area of water deeper than 100 fathoms (183 m), is a possible summer habitat of *Paralithodes camtschatica*. Captain Cove, the site of an earlier record, also adjoins Ogden Channel.

OCCURRENCE OF *LITHODES AEQUISPINA* BENEDICT IN BRITISH COLUMBIA

In early May, 1959, about 30 king crabs were caught by the United States trawler *Dakota* (Captain E. G. Westman), in Queen Charlotte Sound, British Columbia, approximately 35 miles (65 km) east of Cape St. James and in depths

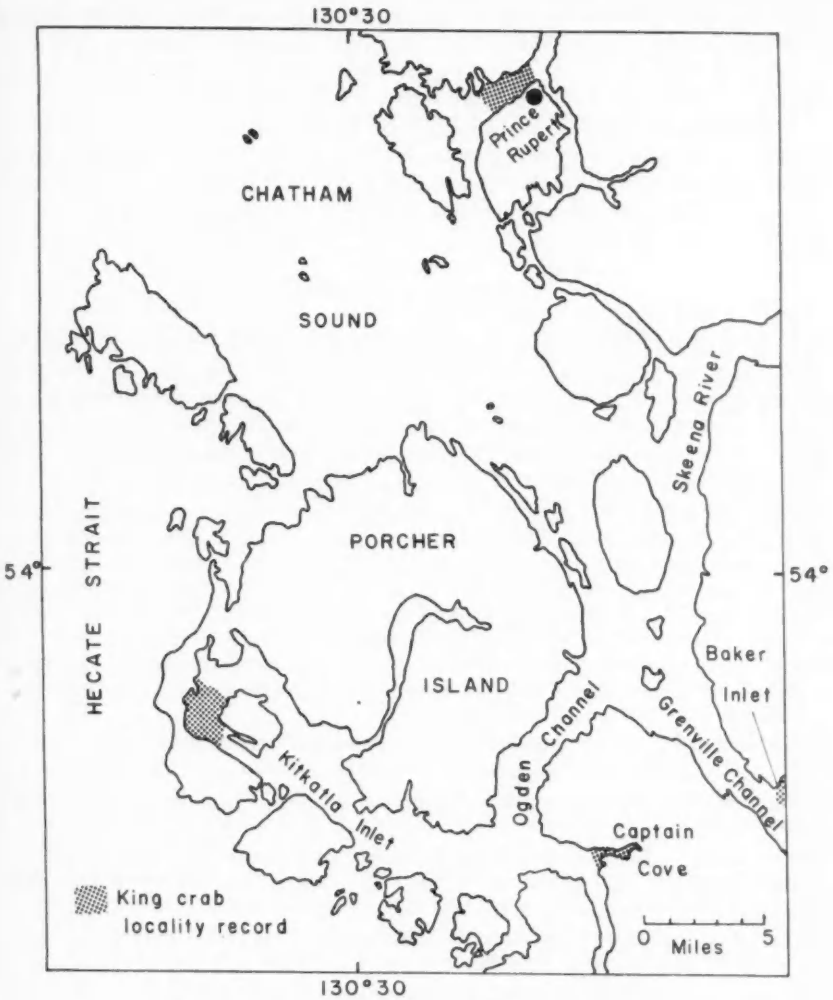

FIG. 6. Map to show locality records of *P. camtschatica* in northern waters of British Columbia.

of 150 to 200 fathoms (275–366 m). One individual was preserved and subsequently identified at the United States National Museum, Washington, as *Lithodes aequispina* Benedict. The specimen is a male with a carapace length of 160 mm and width of 171 mm. On August 31, 1959, the Canadian trawler *Princeton No. I* (Captain G. R. Grossmith) caught another male specimen, 21 miles (39 km) S by SW of Ucluelet, Vancouver Island, in 42 fathoms (77 m).

The carapace measured 187 mm in length and 195 mm in width and the distance between the tips of the extended walking legs was about 40 inches (102 cm). Neither of these specimens differs significantly from the original description of Benedict (1894), nor from the more recent one by Makarov (1938).

The capture of a third male specimen in the fall of 1961 by the United States trawler *Western Flyer* (Captain Dan Luketa), off Sidney Inlet, Vancouver Island, at about 200 fathoms (360 m) has been reported to us by Mr T. Miyahara of Seattle. Measurements which he obtained of the carapace were 178 mm in length and 194 mm in width.

ACKNOWLEDGMENTS

We wish to thank Miss P. A. McLaughlin of Seattle, who gave us the opportunity of recording the first specimen of *Lithodes aequispina* and who was most helpful with regard to the literature. We want also to express our appreciation to Dr R. E. Foerster, Biological Station, Nanaimo, British Columbia, for his help in translation and to Mr John A. Thomson, who made special efforts to collect specimens in Kitkatla Inlet while in charge of the *A. P. Knight*. The photographs were taken by Mr C. J. Morley. Specimens, one of each species, have been deposited in the National Museum, Ottawa.

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Changes in Glycogen, Pyruvate and Lactate in Rainbow Trout *Salmo ga irdneri)* During and Following Muscular Activity[1,2,3]

By Edgar C. Black, Anne Robertson Connor, Kwok-Cheung Lam and Wing-Gay Chiu

ABSTRACT

Experiments upon muscular fatigue in 1½-year-old rainbow trout (*Salmo gairdneri*) were carried out at the trout hatchery at Summerland, British Columbia during the summers of 1958 and 1959. Observations were made on hemoglobin, water content of muscle and whole blood, muscle and liver glycogen, and pyruvate and lactate in muscle, blood and liver. Experimental conditions included 30 min moderate activity, 2–15 min severe exercise, and recovery up to 24 hr following 15 min severe exercise. The results for hemoglobin, muscle and liver glycogen and blood lactate were similar to those reported earlier. Muscle glycogen was depleted 50% or more in the first 2 min of severe activity. Correlated with this rapid depletion of glycogen was a sudden accumulation of muscle pyruvate and lactate. Pyruvate and lactate likewise increased in the blood. While the disappearance of both pyruvate and lactate from muscle began immediately upon cessation of activity, resting levels were not approached until the 8th hr of recovery. During recovery, the levels of pyruvate and lactate in the blood after severe exercise continued to increase for the first hour, remained elevated for at least 8 hr and did not return to the resting level until the 12th–24th hr. Muscle glycogen was not restored above half the resting level at the end of 24 hr. Interpretations of the data in relation to metabolism in rainbow trout are discussed.

INTRODUCTION

The pattern of immediate changes in carbohydrate metabolism in fishes following muscular activity is similar to that in other vertebrates including mammals (Drummond and Black, 1960; Black *et al.*, 1961). Muscle glycogen breaks down during severe exercise (Miller *et al.*, 1959; Black *et al.*, 1960), and lactate appears in great quantity both in the blood (von Buddenbrock, 1938; Secondat and Diaz, 1942; Leivestad *et al.*, 1957; Nakatani, 1957; Black, 1955, 1957a,b,c; Black *et al.*, 1959; Parker and Black, 1959; Parker *et al.*, 1959; Miller *et al.*, 1959; Black *et al.*, 1960) and in the muscle (Nakatani, 1957; Leivestad *et al.*, 1957). The rate of disappearance of lactate in fishes during recovery from severe exercise is slow as compared with mammals (Secondat and Diaz, 1942; Black, 1957a, b,c; Parker and Black, 1959; Parker *et al.*, 1959; Black *et al.*, 1959, 1960). This slower rate may be due to decreased diffusion rates at low temperatures, or to inadequate oxygenation and other effects of reduced circulation, or to both.

The present paper deals with the rate of breakdown of glycogen, the rate of appearance of lactate and its precursor, pyruvate, in muscle, blood and liver

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[2]Contribution from the Department of Physiology, University of British Columbia, Vancouver, Canada, and the Fish and Game Branch of the Department of Recreation and Conservation, Province of British Columbia.

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and with the rate of removal of accumulated pyruvate and lactate from the body. The implications of the changes in carbohydrate metabolism relative to muscular activity in fishes are discussed.

METHODS AND MATERIALS

The experiments were carried out during the summers of 1958 and 1959 at the trout hatchery operated by the Fish and Game Branch of the British Columbia Department of Recreation and Conservation at Summerland, British Columbia. The fish used were 1½-year-old hatchery-raised fall-spawning rainbow trout (*Salmo gairdneri*). In 1958 the diet consisted of ground mammalian viscera. The following year Clark's pelletted dry rations were used. The fish were fed each morning including the day of the experiment, and in all cases were in an unexercised condition prior to the experiments.

Exercise was carried out as described in earlier papers (Black, 1955, 1957a; Black *et al.*, 1960). Groups of fish were sampled in the unexercised condition and after 2–15 min severe exercise in both years. In 1958, additional groups were sampled after 30 min moderate exercise in a rotating chamber at 18.9±1.71 m/min (62.0±5.65 ft/min), and after ½ to 24 hr recovery from 15 min severe exercise. No fish was sampled more than once.

The methods of obtaining blood and tissue samples were those described in the papers cited above. In many cases, blood and tissue samples were taken from different fish in order to reduce the handling time for samples.

In 1958, the technique of quick-freezing muscle and liver samples was instituted. Immediately upon excision, the tissue samples were placed in a freezing mixture of dry-ice and 95% ethanol. Aliquots were weighed and prepared for analysis in the frozen state.

Samples of frozen muscle and liver for glycogen determination were digested in boiling 30% KOH immediately after weighing. The KOH digests were stored at room temperature for several months until assayed.

For lactate and pyruvate determinations, 1–2 g of muscle or liver were ground in a chilled mortar for 10 min in 10 ml of cold trichloracetic acid. In 1959, the extracts were prepared by homogenization in a Servall Omni-Mixer (5 min at slow speed followed by 1 min at high speed) with the cup immersed in a cold water bath. A comparison of muscle lactate values obtained by the two methods has been made. Tissue homogenates were filtered in the cold room and the filtrates stored at 5°C until analyzed.

Hemoglobin was determined as described by Black (1955). Lactate levels were determined on the trichloracetic acid filtrates of blood, muscle and liver within 24 hr of sampling by the method of Barker and Summerson (1941). Glycogen was assayed by the phenol-sulphuric acid method of Montgomery (1957). Pyruvate levels were determined by the method of Friedemann and Haugen (1943) as modified by Sacks *et al.* (1954) on trichloracetic acid filtrates which had stood overnight at 3–5°C.

Water content of whole blood and unfrozen muscle from unexercised fish was estimated in 1959 by drying weighed samples at 90–110°C for 5 days and reweighing.

In 1959, a comparison was made of lactate and glycogen levels in frozen muscle cores taken from 3 discrete anatomical positions in fish strenuously exercised for 2 min. The 3 positions, all above the lateral line, were: (1) *front*, immediately behind the grills (corresponding to the sample taken for analysis in all other experiments), (2) *middle*, below the leading edge of the dorsal fin, and (3) *tail*, just in front of the adipose fin.

RESULTS AND DISCUSSION

Comparison of Methods of Tissue Extraction

The results of a direct comparison between the use of a Servall Omni-Mixer and the method of hand-grinding formerly used for homogenizing and extracting muscle are presented in Table I. The Servall method gives muscle lactate values

Table I. Comparative levels of lactate in frozen muscle homogenized by Servall Omni-mixer for 6 min and by hand in a mortar for 10 min. Unexercised 1½-year-old rainbow trout. 11.5°C. 1960.

	Muscle lactate	
	Servall (6 min)	Mortar (10 min)
	mg/100 g	*mg*/100 g
Mean ± SE	108 ± 7.9	66 ± 5.3
(n)	(17)	(17)
Range	47–178	19–97

which average about 60% higher than the hand-grinding method. This may account for the consistently higher muscle lactate levels found in 1959 as compared to 1958 (Tables IV, V, VI). The values obtained in 1959 are close to those reported by Nakatani (1957) for adult steelhead trout using a de Vertis homogenizer. The average unexercised level found by Nakatani was 174 mg/100 g and the level after an average of 8.5 min exercise was 389 mg/100 g.

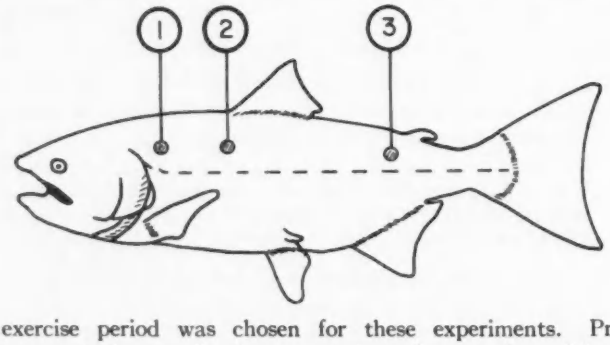
The possibility has not been eliminated that the higher lactate values obtained with the Servall are due to a greater degree of autolysis during grinding. Determination of glycogen levels in the trichloracetic acid filtrates would clarify this point.

Lactate and Glycogen Levels in Different Anatomical Sites

The possibility was considered that certain sections of the body, especially near the tail, might be more active during the process of swimming and therefore show a higher rate of glycolysis. Muscle lactate and glycogen levels in core samples from three different anatomical sites are compared in Table II. A

TABLE II. Comparison of muscle glycogen and lactate levels from three different anatomical positions in 1½-year-old rainbow trout (see below), after 2 minutes, strenuous exercise. 11.5°C, 1959.

		Position (1) *front*	Position (2) *middle*	Position (3) *tail*
Muscle glycogen (% wet wt.)	Mean ± SE	0.04±0.009	0.07±0.014	0.09±0.014
	(n)	(12)	(12)	(12)
	Range	0.02–0.14	0.02–0.20	0.03–0.20
Muscle lactate (mg/100 g wet wt)	Mean ± SE	438±24.1	523±25.4	533±34.6
	(n)	(12)	(12)	(12)
	Range	228–529	287–621	211–703
Ratio lactate/glycogen (based on individual samples)		14/1	12/1	8/1



2-minute exercise period was chosen for these experiments. Progressively higher lactate and glycogen levels are noted as the sample position is located nearer the tail. However, the ratio of lactate to glycogen decreases in this direction, therefore there is no indication that greater muscular activity is taking place in the tail section. The possible error introduced by the routine use of the *front* position (1) for muscle sampling is considered negligible.

WATER CONTENT OF MUSCLE AND BLOOD

Measurements were made of the water content of unfrozen muscle and whole blood of unexercised and severely exercised trout (Table III).

TABLE III. Water content of fresh muscle and whole blood in 1½-year-old rainbow trout in the unexercised condition and during 15 min strenuous exercise. 11.5°C, 1959.

		Unexercised	Strenuous exercise			
			2 min	5 min	9 min	15 min
Muscle water content (% wet wt)	Mean±SE	76.26±0.151	76.29±0.142	76.51±0.131	76.11±0.264	76.46±0.165
	(n)	(21)	(23)	(11)	(11)	(13)
	Range	75.09–77.28	74.89–77.48	75.99–77.34	75.21–78.03	75.22–77.57
Whole blood water content (%)	Mean±SE	86.31±0.358	84.97±0.391	84.72±0.581	83.10±0.536	83.23±0.378
	(n)	(21)	(19)	(11)	(11)	(13)
	Range	83.08–89.91	81.61–88.62	82.98–89.64	80.74–86.33	80.85–85.07

A slight (3%) decrease in the average blood water content was noted after 15 min exercise. No change was observed in muscle water content. The change in blood water may account for the rise in hemoglobin concentration

commonly seen in fish during severe exertion (Black *et al.*, 1959). It is not sufficient, however, to account for changes in other blood constituents (lactate, pyruvate, glucose, etc.) which may increase 5-fold or more in the same period.

The shift of water from the circulation does not appear to be in the direction of engorgement of the tissues and does not seem to be great enough to indicate that any degree of shock due to loss of blood fluid accompanies severe exercise in trout. However, there is still the possibility that shock due to circulatory collapse and loss of effective circulating blood volume may occur. This is indeed probable since it has been noted repeatedly that it is much more difficult to obtain blood from the heart in exercised than in unexercised or recovered fish.

Unexercised, Exercised and Recovery States — 1958 Data

Body weights. Body weights of the rainbow trout used in the 1958 experiments are given in Tables IV and V. The overall average weight for the 188 fish used was 146±3.7 g with a range of 52–332 g. The average weight of the male fish was 142±4.5 g and of the female fish 151±5.9 g. The difference between male and female body weights was not statistically significant.

Hemoglobin. The hemoglobin level for the rested condition in 1958 was 10.2 g% (Table IV). This value is not significantly different from those obtained in 1957 for 2-year-old Kamloops trout spawners (Black *et al.*, 1960), but it is lower than for the 1½-year-old rainbow trout reported in that paper.

The course of the hemoglobin changes during exercise and recovery in 1958 (Tables IV and V) was similar to the 1957 findings with the exception of the initial value. Blood hemoglobin concentrations were rapidly elevated under conditions of severe exercise, probably reaching maxima at about 5 minutes. It was noted in earlier work (Black *et al.*, 1959) that the sharpest increase in hydrogen ion concentration was during this same time interval.

The hemoglobin level remained elevated throughout the course of exercise and recovery. As noted above, the elevated hemoglobin may be associated with a decrease in blood water content.

Although the data are too few to draw definite conclusions, nonetheless there is a consistently higher hemoglobin level observed in males than in females during both moderate and severe exercise, and during recovery from severe exercise.

Muscle glycogen. The resting value for muscle glycogen in 1958 was 0.25% wet weight (Table IV), a value which is nearly 3 times that reported earlier for rainbow trout of the same age (Black *et al.*, 1960). It is probable that the higher level is due to the use in 1958 of the technique of quick-freezing tissues immediately upon excision. Black *et al.*, (1960) have shown by direct experiment that autolysis of muscle glycogen in unfrozen excised tissues may amount to 30% of the initial level in 5 min.

Extremely rapid breakdown of muscle glycogen during severe activity is illustrated in Fig. 1a (see also Table IV). The level was reduced by ½ within 2 min and by ⅝ within 15 min of the commencement of exercise.

TABLE IV. Body weights and levels of hemoglobin; muscle and liver glycogen; and muscle, blood and liver pyruvate and lactate in 1½-year-old rainbow trout in the unexercised condition, after 30 minutes moderate exercise in a rotating chamber (cruising speed 18.9±1.71 m/min) and during 15 minutes strenuous exercise. 11.5°C, 1958.

		Unexercised	Moderate exercise 30 min	Strenuous exercise 2 min	Strenuous exercise 5 min	Strenuous exercise 9 min	Strenuous exercise 15 min
Body Weight (*grams*)	Mean ±SE	148±13.7	153±10.3	143±14.5	136±11.3	150±13.0	161±19.7
	(n)	(18)	(16)	(16)	(16)	(13)	(11)
	Range	52–312	111–231	81–279	100–281	101–245	71–321
	Male mean (n)	157 (11)	148 (6)	129 (9)	120 (6)	154 (6)	156 (6)
	Female mean (n)	148 (6)	151 (9)	161 (7)	157 (8)	146 (7)	166 (5)
Hemoglobin (*grams %*)	Mean ±SE	10.2±0.66	12.0±0.53	12.8±0.44	14.3±0.94	13.1±0.46	13.7±0.81
	(n)	(8)	(7)	(4)	(5)	(8)	(9)
	Range	8.4–14.0	10.3–13.9	11.9–14.0	12.0–16.8	11.8–16.0	10.7–17.3
	Male mean (n)	10.2 (5)	13.1 (3)	14.0 (1)	14.8 (3)	13.2 (4)	14.5 (6)
	Female mean (n)	10.1 (3)	11.3 (3)	12.4 (3)	13.5 (2)	13.0 (4)	12.1 (3)
Muscle Glycogen (*% wet wt*)	Mean ±SE	0.25±0.049	0.12±0.012	0.11±0.038	0.07±0.018	0.05±0.017	0.04±0.010
	(n)	(8)	(8)	(8)	(8)	(8)	(8)
	Range	0.10–0.51	0.06–0.17	0.02–0.34	0.02–0.13	0.01–0.15	0.01–0.09
	Male mean (n)	0.30 (6)	0.14 (3)	0.17 (5)	0.11 (3)	0.09 (4)	0.05 (4)
	Female mean (n)	0.10 (2)	0.10 (5)	0.02 (3)	0.02 (4)	0.02 (4)	0.02 (4)
Liver Glycogen (*% wet wt*)	Mean ±SE	0.83±0.124	0.82±0.280	1.24±0.264	1.41±0.239	1.81±0.351	0.59±0.101
	(n)	(8)	(8)	(8)	(8)	(8)	(6)
	Range	0.40–1.38	0.26–2.71	0.26–2.29	0.55–2.90	0.69–3.33	0.29–0.88
	Male mean (n)	0.85 (5)	0.69 (3)	1.52 (5)	1.13 (3)	2.57 (4)	0.56 (3)
	Female mean (n)	0.79 (3)	0.90 (5)	0.77 (3)	1.59 (4)	1.04 (4)	0.62 (3)
Muscle Pyruvate (*mg/100 g*)	Mean ±SE	0.91±0.192	1.73±0.320	4.98±1.283	5.63±0.792	5.43±0.537	3.94±0.658
	(n)	(9)	(8)	(8)	(8)	(8)	(8)
	Range	0.16–1.88	0.75–3.17	0.50–9.47	2.70–8.85	3.93–8.43	1.13–6.35
	Male mean (n)	0.78 (6)	1.66 (3)	2.54 (5)	4.19 (3)	4.88 (4)	3.32 (4)
	Female mean (n)	1.18 (3)	1.76 (5)	9.04 (3)	7.32 (4)	5.97 (4)	4.55 (4)
Blood Pyruvate (*mg %*)	Mean ±SE	0.29±0.029	0.55±0.077	0.44±0.079	0.47±0.037	0.55±0.063	0.51±0.044
	(n)	(8)	(8)	(8)	(8)	(8)	(9)
	Range	0.18–0.43	0.28–0.96	0.16–0.84	0.31–0.63	0.37–0.89	0.27–0.67
	Male mean (n)	0.27 (5)	0.36 (3)	0.31 (4)	0.50 (3)	0.43 (4)	0.48 (5)
	Female mean (n)	0.33 (3)	0.59 (4)	0.58 (4)	0.49 (4)	0.66 (4)	0.54 (4)
Liver Pyruvate (*mg/100 g*)	Mean ±SE	0.56±0.095	0.57±0.059	0.45±0.085	0.49±0.066	0.60±0.137	0.28±0.103
	(n)	(8)	(8)	(8)	(8)	(8)	(7)
	Range	0.23–0.95	0.35–0.83	0.23–0.99	0.17–0.79	0.15–1.19	0.08–0.89
	Male mean (n)	0.64 (5)	0.54 (3)	0.55 (5)	0.55 (3)	0.92 (4)	0.40 (3)
	Female mean (n)	0.42 (3)	0.59 (5)	0.29 (3)	0.42 (4)	0.27 (4)	0.19 (4)
Muscle Lactate (*mg/100 g*)	Mean ±SE	66±14.4	84±7.9	224±33.3	249±36.1	294±20.0	295±27.1
	(n)	(9)	(8)	(8)	(8)	(8)	(8)
	Range	15–162	49–113	119–344	111–399	219–381	183–394
	Male mean (n)	63 (6)	68 (3)	159 (5)	188 (3)	257 (4)	261 (4)
	Female mean (n)	72 (3)	94 (5)	334 (3)	330 (4)	323 (4)	329 (4)
Blood Lactate (*mg %*)	Mean ±SE	4.0±0.61	13.5±3.12	23.1±2.50	42.5±4.02	52.5±5.69	54.0±5.98
	(n)	(9)	(8)	(8)	(8)	(8)	(10)
	Range	2.0–7.5	3.4–29.1	14.6–32.0	21.9–54.8	30.4–76.6	20.0–88.8
	Male mean (n)	3.5 (5)	6.3 (3)	17.3 (4)	38.5 (3)	39.9 (9)	46.3 (6)
	Female mean (n)	4.7 (4)	15.0 (4)	28.8 (4)	50.5 (4)	65.0 (4)	65.5 (4)
Liver Lactate (*mg/100 g*)	Mean ±SE	19.7±1.70	24.6±2.02	24.4±3.24	34.0±3.22	35.8±4.27	45.5±3.16
	(n)	(9)	(8)	(8)	(8)	(8)	(8)
	Range	11.9–26.5	18.2–33.6	15.7–41.5	19.0–46.2	21.8–54.0	25.5–56.5
	Male mean (n)	21.3 (6)	20.6 (3)	26.4 (5)	37.5 (3)	37.8 (4)	44.0 (4)
	Female mean (n)	16.4 (3)	27.1 (5)	21.1 (3)	31.6 (4)	33.9 (4)	47.0 (4)

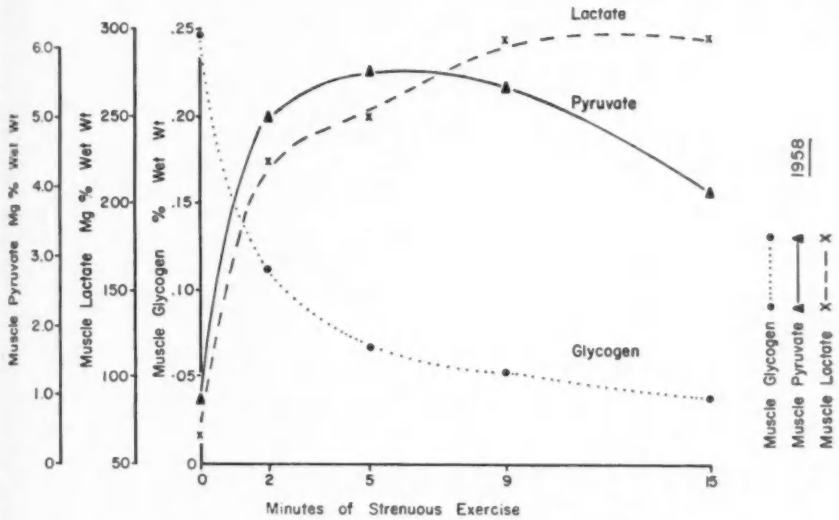


FIG. 1a. Changes in muscle levels of glycogen, pyruvate and lactate during 15 min strenuous exercise in 1½-year-old rainbow trout. 11.5°C, 1958.

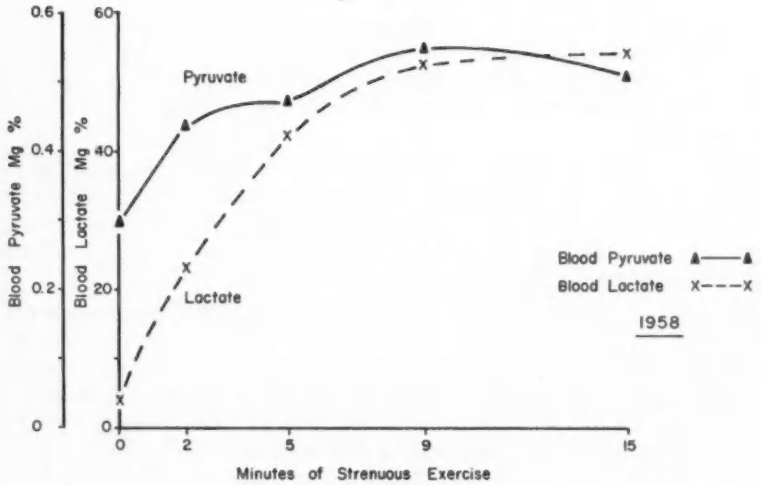


FIG. 1b. Changes in blood levels of pyruvate and lactate during 15 min strenuous exercise in 1½-year-old rainbow trout. 11.5°C, 1958.

FIG. 1c. Changes in liver levels of glycogen, pyruvate and lactate during 15 min strenuous exercise in 1½-year-old rainbow trout. 11.5°C, 1958.

The muscle glycogen level after 30 min moderate exercise (steady state) was 0.12%, a reduction of 50% from the pre-exercise level (Table IV). In the work reported by Black *et al.*, (1960), the steady state values were actually higher than the resting value. The fish reported here struggled to a greater degree in the rotating chamber probably because of their larger size. The average weight of the 1958 steady state fish was 153 g (Table IV) as compared to 112 g in 1957.

Recovery of muscle glycogen during the first 24 hours after severe exercise was most variable (Fig. 2, Table V). During the first 30 min of recovery the muscle glycogen was restored to approximately one-third of the resting value. Despite the variability of the level in the succeeding 24 hrs it did not differ greatly from the value achieved at 30 min.

The level of muscle glycogen in male fish in the 1958 experiments was 3 times as high as that in females. During severe exercise, the initially higher glycogen level in males was depleted more slowly. A 44% reduction occurred in the first 2 min, and an 82% reduction by the end of 15 min. In females the depletion was 76% at the 2 min interval and the level remained practically unchanged from that for the remainder of the exercise period. During 30 min moderate exercise, the muscle glycogen level in males fell 52% while that in females remained about the same as the initial resting value. In recovery from severe exercise, the muscle glycogen appeared to be restored somewhat more quickly in males than in females (Table V).

TABLE V. Body weights and levels of hemoglobin; muscle and liver glycogen; and muscle, blood and liver pyruvate and lactate in 1½-year-old rainbow trout during 24 hours recovery from 15 minutes strenuous exercise. 11.5°C, 1958.

		30 min	1 hour	2 hours	3 hours	4 hours	6 hours	8 hours	12 hours	24 hours
Body Weight (*grams*)	Mean ±SE	151 ±11.6	143 ±11.4	170 ±30.5	125 ±12.4	121 ±14.4	147 ±13.1	135 ±11.1	176 ±19.3	136 ±10.4
	(n)	(10)	(10)	(7)	(12)	(8)	(11)	(15)	(12)	(13)
	Range	112–214	76–205	98–332	77–243	62–182	96–224	67–226	95–321	103–249
	Male mean (n)	149 (5)	140 (5)	150 (4)	138 (7)	110 (4)	152 (5)	133 (6)	160 (6)	127 (8)
	Female mean (n)	153 (5)	146 (5)	198 (3)	107 (5)	133 (4)	143 (6)	136 (9)	193 (6)	149 (5)
Hemoglobin (*grams %*)	Mean ±SE	13.4 ±0.89	13.5 ±0.50	14.5 ±0.95	13.8 ±0.68	13.7 ±0.72	12.7 ±0.79	11.6 ±1.11	13.0 ±0.99	12.7 ±0.83
	(n)	(7)	(7)	(6)	(4)	(6)	(5)	(6)	(5)	(7)
	Range	8.9–16.4	11.8–15.5	11.5–18.2	12.9–15.8	11.5–16.0	10.5–14.4	9.2–15.7	10.0–15.4	10.1–16.4
	Male mean (n)	13.4 (4)	14.0 (3)	15.2 (4)	14.1 (3)	15.2 (3)	12.0 (3)	14.9 (2)	13.6 (2)	13.3 (5)
	Female mean (n)	13.4 (3)	13.2 (4)	13.3 (2)	12.9 (1)	12.2 (3)	13.7 (2)	9.9 (4)	12.6 (3)	11.1 (2)
Muscle Glycogen (*% wet wt*)	Mean ±SE	0.10 ±0.033	0.05 ±0.021	0.08 ±0.054	0.08 ±0.016	0.06 ±0.022	0.06 ±0.007	0.09 ±0.015	0.10 ±0.014	0.10 ±0.014
	(n)	(7)	(6)	(6)	(9)	(6)	(7)	(8)	(6)	(6)
	Range	0.02–0.21	0.02–0.15	0.02–0.35	0.02–0.16	0.02–0.17	0.04–0.09	0.04–0.15	0.05–0.15	0.07–0.16
	Male mean (n)	0.15 (4)	0.07 (3)	0.14 (3)	0.09 (6)	0.10 (3)	0.07 (3)	0.13 (3)	0.12 (4)	0.12 (3)
	Female mean (n)	0.02 (3)	0.03 (3)	0.03 (3)	0.04 (3)	0.03 (3)	0.05 (4)	0.06 (5)	0.06 (2)	0.08 (3)
Liver Glycogen (*% wet wt*)	Mean ±SE	1.74 ±0.639	1.01 ±0.262	1.09 ±0.374	0.82 ±0.151	1.38 ±0.312	0.67 ±0.195	1.14 ±0.362	0.84 ±0.099	0.94 ±0.114
	(n)	(7)	(6)	(6)	(9)	(6)	(7)	(8)	(6)	(6)
	Range	0.53–5.27	0.26–1.67	0.20–2.33	0.24–1.61	0.53–2.33	0.24–1.66	0.33–3.15	0.55–1.22	0.53–1.22
	Male mean (n)	2.16 (4)	1.17 (3)	0.93 (3)	0.80 (6)	1.63 (3)	0.94 (3)	1.38 (3)	0.95 (4)	0.88 (3)
	Female mean (n)	1.17 (3)	0.84 (3)	1.24 (3)	0.86 (3)	1.13 (3)	0.46 (4)	1.00 (5)	0.60 (2)	0.99 (3)
Muscle Pyruvate (*mg/100 g*)	Mean ±SE	5.09 ±0.697	5.61 ±0.882	5.15 ±1.386	2.95 ±0.438	1.65 ±0.248	0.96 ±0.229	1.44 ±0.416	0.67 ±0.161	1.37 ±0.333
	(n)	(7)	(6)	(6)	(9)	(6)	(6)	(8)	(6)	(6)
	Range	1.54–7.07	2.75–8.42	0.67–10.73	0.52–4.26	0.66–2.33	0.36–1.90	0.41–3.36	0.20–1.27	0.34–2.60
	Male mean (n)	4.08 (4)	5.04 (3)	4.04 (3)	2.91 (6)	1.19 (3)	0.55 (3)	0.67 (3)	0.44 (4)	0.85 (3)
	Female mean (n)	6.43 (3)	6.19 (3)	6.27 (3)	3.03 (3)	2.11 (3)	1.37 (3)	1.91 (5)	1.13 (2)	1.89 (3)
Blood Pyruvate (*mg %*)	Mean ±SE	1.17 ±0.182	1.54 ±0.134	1.48 ±0.214	1.43 ±0.163	1.41 ±0.183	1.12 ±0.176	0.95 ±0.135	0.46 ±0.041	0.30 ±0.035
	(n)	(7)	(7)	(7)	(6)	(6)	(6)	(7)	(6)	(7)
	Range	0.33–1.61	1.10–1.98	0.54–2.01	0.93–1.98	1.00–2.10	0.68–1.84	0.50–1.67	0.36–0.63	0.19–0.43
	Male mean (n)	0.90 (4)	1.18 (3)	1.12 (4)	1.11 (3)	1.06 (3)	0.81 (3)	0.71 (3)	0.39 (2)	0.31 (5)
	Female mean (n)	1.54 (3)	1.81 (4)	1.97 (3)	1.76 (3)	1.77 (3)	1.43 (3)	1.13 (4)	0.49 (4)	0.26 (2)
Liver Pyruvate (*mg/100 g*)	Mean ±SE	0.45 ±0.068	0.63 ±0.126	0.65 ±0.067	0.51 ±0.089	1.11 ±0.214	0.72 ±0.040	0.98 ±0.125	0.64 ±0.057	0.55 ±0.050
	(n)	(6)	(6)	(6)	(9)	(6)	(7)	(8)	(6)	(6)
	Range	0.20–0.70	0.19–0.99	0.45–0.85	0.11–0.79	0.65–2.00	0.51–0.86	0.55–1.61	0.37–0.76	0.33–0.70
	Male mean (n)	0.40 (3)	0.73 (3)	0.72 (3)	0.43 (6)	0.93 (3)	0.72 (3)	1.31 (3)	0.61 (4)	0.49 (3)
	Female mean (n)	0.51 (3)	0.53 (3)	0.58 (3)	0.65 (3)	1.29 (3)	0.72 (4)	0.78 (5)	0.69 (2)	0.61 (3)
Muscle Lactate (*mg/100 g*)	Mean ±SE	256 ±35.9	244 ±15.9	249 ±33.2	167 ±16.9	191 ±27.4	92 ±15.1	61 ±11.0	52 ±9.6	57 ±8.9
	(n)	(7)	(6)	(6)	(9)	(6)	(6)	(8)	(6)	(6)
	Range	111–369	196–303	119–323	93–241	136–309	48–144	29–107	28–89	28–93
	Male mean (n)	257 (4)	230 (3)	192 (3)	165 (6)	150 (3)	93 (3)	36 (3)	42 (4)	45 (3)
	Female mean (n)	255 (3)	257 (3)	306 (3)	171 (3)	233 (3)	90 (3)	75 (5)	72 (2)	69 (3)
Blood Lactate (*mg %*)	Mean ±SE	77.1 ±14.27	108.9 ±7.92	108.4 ±19.14	104.2 ±16.32	143.9 ±31.40	78.9 ±16.92	45.9 ±12.85	8.7 ±0.43	4.3 ±0.35
	(n)	(7)	(7)	(7)	(7)	(6)	(6)	(7)	(6)	(6)
	Range	23.1–127.7	76.3–134.6	23.1–164.9	20.8–136.6	79.6–273.5	32.8–148.4	14.6–95.4	7.0–10.1	3.1–5.6
	Male mean (n)	55.1 (4)	93.8 (3)	78.3 (4)	79.6 (4)	94.8 (3)	56.7 (3)	23.3 (3)	8.0 (2)	3.9 (5)
	Female mean (n)	106.4 (3)	120.3 (4)	148.6 (3)	137.1 (3)	192.9 (3)	101.2 (3)	62.9 (4)	9.0 (4)	5.0 (2)
Liver Lactate (*mg/100 g*)	Mean ±SE	66.4 ±7.51	72.6 ±10.43	71.4 ±11.72	61.4 ±9.09	98.9 ±14.46	53.8 ±5.20	44.7 ±8.76	24.7 ±3.17	21.8 ±1.38
	(n)	(7)	(6)	(6)	(9)	(6)	(7)	(8)	(6)	(6)
	Range	40.5–101.0	48.4–119.4	19.9–102.6	15.0–97.5	67.7–154.6	29.0–62.9	24.3–103.1	16.0–35.6	17.9–26.5
	Male mean (n)	56.1 (4)	66.7 (3)	57.1 (3)	61.2 (6)	81.0 (3)	61.9 (3)	38.3 (3)	25.4 (4)	19.2 (3)
	Female mean (n)	80.1 (3)	78.4 (3)	85.7 (3)	61.8 (3)	116.9 (3)	47.7 (4)	48.5 (5)	23.2 (2)	24.4 (3)

LIVER GLYCOGEN. The liver glycogen values for 1958 are summarized in Tables IV and V and illustrated in Fig. 1c and 2. The resting level is about half of that recorded for the 1957 series (Black *et al.*, 1960). There was an apparent increase in the liver glycogen during the first 9 min of strenuous exercise followed by a sharp drop from the 9th to the 15th minute. However, owing to the high degree of variation between individual liver samples (note large standard

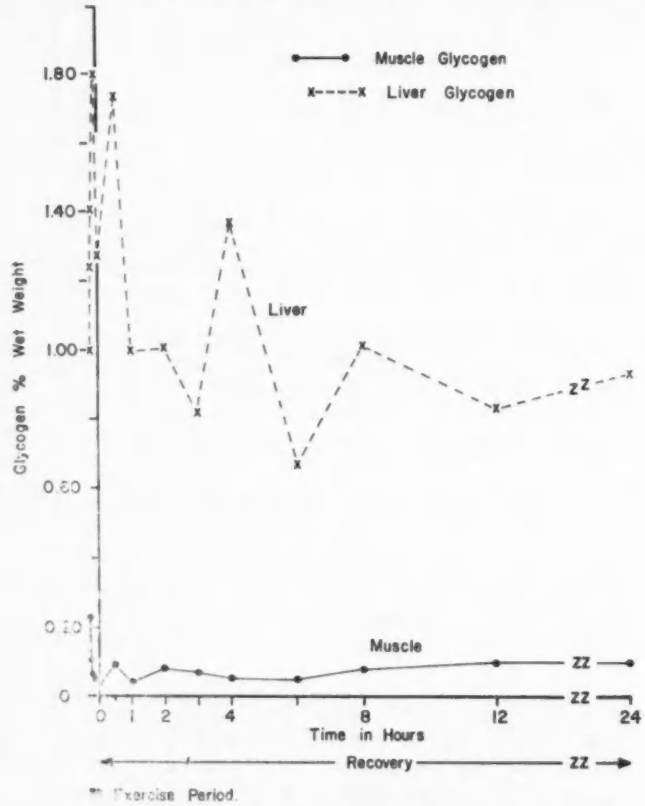


FIG. 2. Changes in muscle and liver levels of glycogen during 15 min strenuous exercise and 24 hours recovery in 1½-year-old rainbow trout. 11.5°C, 1958.

errors in Tables IV and V), it is doubtful that the experimental groups are large enough to permit the detection of any real differences due to exercise. The range of liver glycogen levels during recovery is even more variable. During the 1957 experiments (Black *et al.*, 1960) the recovery values for liver glycogen showed a progressive decline following vigorous exercise. This was interpreted as a reflection of the fact that the fish were not fed during recovery. The same pattern was not observed in the 1958 experiments.

In contrast to the differences noted in muscle glycogen between male and female fish, the level of glycogen in the liver was nearly the same in both sexes in all conditions.

MUSCLE PYRUVATE. The resting value of muscle pyruvate in 1958 was 0.91 mg per 100 g wet tissue (Table IV). This value is slightly higher than those reported by Sacks *et al.*, (1954) for resting frog muscle and by Sacks and Morton (1956) for resting cat muscle.

During steady state activity, the level in rainbow trout increased to 1.73 mg/100 g (Table IV). This is again higher than the value reported by Sacks and Morton (1956) for isolated cat muscle in the steady state, although their period of stimulation was considerably shorter than that used here.

In the first 2 min of severe exercise in trout the increase in muscle pyruvate was 5-fold and at the 5th minute it was 6-fold (Fig. 1a). The peak level at this time was 5.63 mg/100 g. This compares favourably with the values found by Sacks and Morton (1956) in tetanized cat muscle, and by Sacks *et al.*, (1954) in tetanized frog muscle. With continued severe exercise, the muscle pyruvate level in rainbow trout began to drop, and at the end of 15 min activity it was 3.94 mg/100 g, or an approximate 4-fold increase over the resting value (Fig. 1a).

As shown in Table IV and Fig. 3, the muscle pyruvate rose again during the 1st hour of recovery, until it was nearly equal to the peak level during exercise, and did not decrease significantly until the 4th hour of recovery. The lowest level of muscle pyruvate was reached following 12 hrs of recovery. At the end of 24 hrs, the value was not significantly higher than the initial unexercised condition.

In accordance with its role as an intermediary metabolite in the breakdown of glycogen to lactate, muscle pyruvate increased rapidly with muscular exercise during the same interval when muscle glycogen decreased significantly (Fig. 1a).

Muscle pyruvate was consistently higher in female than in male fish, and the rate of increase of pyruvate with severe exercise was likewise greater in female fish.

BLOOD PYRUVATE. Blood levels of pyruvate for 1958 are shown in Tables IV and V and in Fig. 1b and 3. The resting value for rainbow trout was 0.29 mg%. This value is considerably lower than the values recorded for various mammals in the resting condition (Johnson and Edwards, 1937; Lu, 1939; Bueding *et al.*, 1942; Sacks and Morton, 1956; Huckabee, 1958).

During 30 min steady state exercise in trout, there was a 2-fold increase in blood pyruvate. Sacks and Morton (1956) found no appreciable rise in the venous plasma level in cats during steady state stimulation, but as has been noted, their period of stimulation was very short and there is reason to believe that the diffusion of pyruvate from muscle to blood may be relatively slow.

The blood pyruvate level in trout had begun to rise after 2 min of strenuous exercise and was nearly double the resting value after 15 min (Fig. 1b). The rise of blood pyruvate continued during recovery until a 5-fold increase was reached at the 1st hr after the cessation of activity (Fig. 3). Thereafter, the level declined

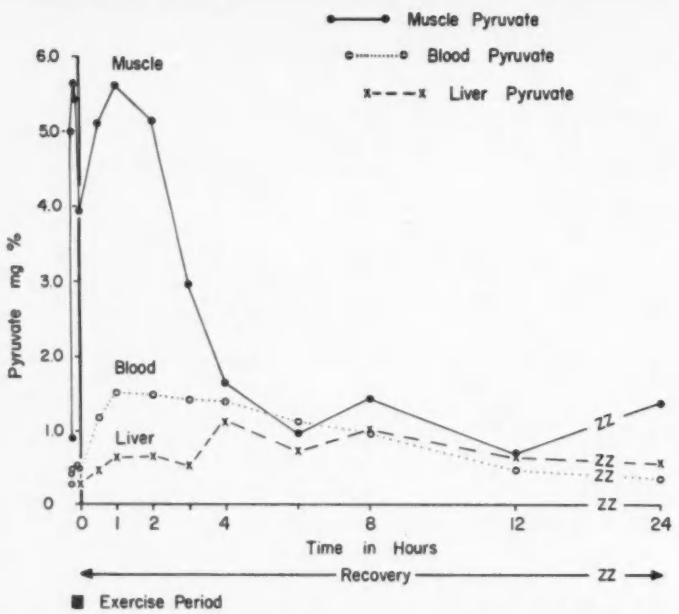


FIG. 3. Changes in muscle, blood and liver levels of pyruvate during 15 min strenuous exercise and 24 hours recovery in 1½-year-old rainbow trout. 11.5°C, 1958.

slowly and showed no major reduction until the 6th hr of recovery. The resting level was not reached until 24 hrs. These findings are similar to those of Johnson and Edwards (1937) in human subjects except that the time course of recovery is greatly extended in trout. Recovery in man was rapid and the pre-exercise pyruvate level was approached by the end of 40 min. The prolonged elevation of the blood pyruvate level in trout parallels the elevation of lactate noted previously (Black, 1957a,b,c; Black *et al.*, 1959, 1960).

Blood pyruvate was higher in female than in male fish for most conditions, reflecting the higher level in the muscle of females.

LIVER PYRUVATE. The resting level of liver pyruvate was 0.56 mg/100g wet tissue (Table IV). This value was practically unchanged during 30 min steady state exercise, and decreased to 0.28 mg/100 g during 15 min of strenuous exercise (Fig. 1c). During the recovery period, the liver pyruvate increased until it was double the resting value at 4 hrs (Table V, Fig. 3), and did not return to the pre-exercise value until 24 hrs following exercise.

In contrast to the findings in muscle and blood, the pyruvate level in liver was frequently considerably higher in males than in females.

MUSCLE LACTATE. Muscle lactate in the resting state averaged 66 mg/100 g wet tissue. This value is considerably higher than those reported in the literature for mammals (Sacks and Sacks, 1937; Sacks and Morton, 1956), frogs (Sacks *et al.*, 1954) and codfish (Leivestad *et al.*, 1957). It is however, much

lower than the resting level in steelhead trout reported by Nakatani (1957) and the level reported below for rainbow trout in 1959. The probable reason for this difference has been discussed.

The muscle lactate level during 30 min steady state activity was 84 mg/100 g (Table IV). This is lower than the values found in isolated mammalian muscle despite the shorter stimulation period used in the latter preparations (Sacks and Sacks, 1937; Sacks and Morton, 1956).

During the first 2 min of vigorous activity the muscle lactate level in rainbow trout rose to 224 mg/100 g, and then increased still further until a level of 295 mg/100 g was reached at the end of 15 min (Table IV, Fig. 1a). Immediately after cessation of activity, the muscle lactate began to subside slowly, and at the 3rd hr of recovery a level of 167 mg/100 g was reached. The pre-exercise level was not attained until the 8th hr of recovery (Fig. 4).

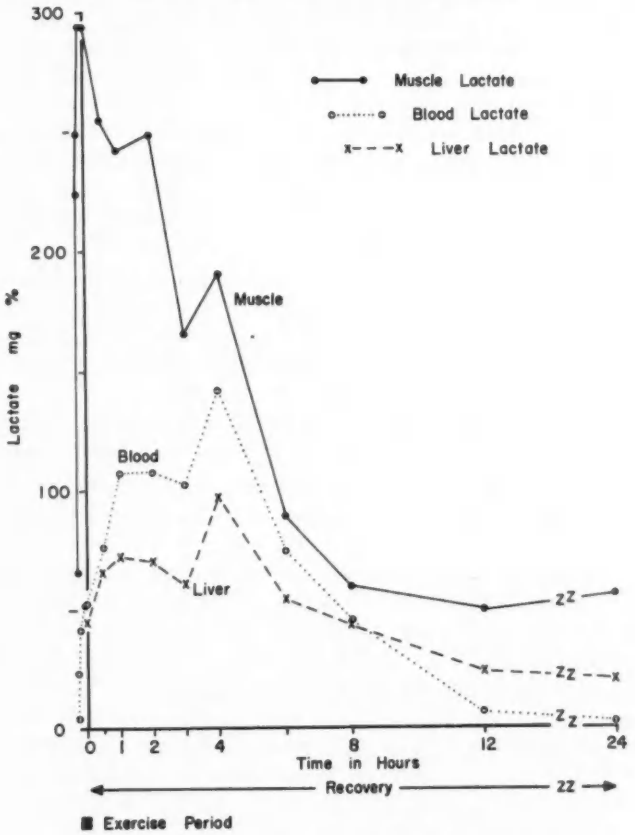


FIG. 4. Changes in muscle, blood and liver levels of lactate during 15 min strenuous exercise and 24 hours recovery in 1½-year-old rainbow trout. 11.5°C, 1958.

The average muscle lactate in females in the 1958 experiments was higher than in males in most conditions. The rate of increase of muscle lactate during severe exercise was likewise greater in females.

BLOOD LACTATE. The average blood lactate in unexercised fish was 4.0 mg%, a value which is much lower than those reported previously (Black *et al.*, 1959, 1960).

During moderate exercise, the steady state level was 13.5 mg%. While this represents a 3-fold increase over the resting level, it is nevertheless lower than the value obtained in the steady state for yearling Kamloops trout (Black, 1957a), and for 1½-year-old rainbow trout in 1957 (Black *et al.*, 1960).

During severe muscular exercise, the blood level of lactate rose 6-fold in the first 2 min of activity, and then continued to rise until a level of some 13 times the initial resting value was attained at the end of 15 min. However, the average value attained at 15 min exercise was 54.0 mg%, which is a considerably lower value than that reported for Kamloops trout, either yearlings (Black, 1957a; Black *et al.*, 1959) or two-year-olds (Black, 1957a). Only in fully mature spawning Kamloops trout (Black *et al.*, 1960) have blood lactate values in the present low range been encountered. It is possible that the low values may be due to the fact that rainbow trout appeared to be much tamer fish and did not respond to the stimulus of exercise as vigorously as did the Kamloops trout. An indication of the variability in the response of fish was reported for 1½-year-old rainbow trout by Black *et al.*, (1960).

The rate of transfer of lactate from muscle to blood appears to be remarkably rapid (Fig. 1a, 1b). The very rapid transfer of muscle lactate to the blood was first reported for codfish struggling in air by Leivestad *et al.*, (1957). Despite the fact that lactate is transferred rapidly from muscle to blood in rainbow trout, the level in muscle remained much higher than that in blood throughout recovery. The persistently high level of blood lactate during the long recovery period is unquestionably derived from the extremely high level in muscle.

The blood lactate level of females was consistently higher than that of males. This corresponds with the higher muscle lactate level of female fish noted above.

LIVER LACTATE. Liver lactate in the unexercised condition averaged 19.7 mg/100 g wet tissue (Table IV). There was no significant change in this value during 30 min of steady state exercise nor during the first 2 min of strenuous exercise (Table IV, Fig. 1c). The rise in liver lactate during the remainder of the 15 min exercise period and the first 4 hrs of recovery closely paralleled the rise in blood lactate although the peak level at 4 hrs was only 98.9 mg/100 g. Thereafter, the level began to diminish reflecting similar changes in muscle and blood. The liver lactate level probably represents an equilibrium between the metabolic changes occurring in the liver and the transfer of lactate from muscle to liver through the blood.

There was no significant difference in the level of liver lactate between males and females.

Unexercised and Severely Exercised States — 1959 Data

Body weights. Body weights of the rainbow trout used in the 1959 experiments are given in Table VI. The overall average weight for 95 fish was 260 g with a standard error of ±6.1 and a range of 132–418 g. The average weight of male fish was 258±9.0 g and of female fish 263±7.9 g. The difference in weight between male and female fish was again not significant. There is no explanation for the difference in weight between the fish used in 1958 and 1959. Both groups were of the same age and sub-species.

Table VI. Body weights and levels of hemoglobin; muscle and liver glycogen; and muscle and blood pyruvate and lactate in 1½-year-old rainbow trout in the unexercised condition and during 15 minutes strenuous exercise. 11.5°C, 1959.

		Unexercised	Strenuous exercise			
			2 min	5 min	9 min	15 min
Body Weight (grams)	Mean±SE	260±12.4	257±8.3	285±12.6	261±25.2	246±13.4
	(n)	(32)	(28)	(11)	(11)	(13)
	Range	158–418	180–331	215–346	132–400	187–316
	Male mean (n)	261 (13)	246 (16)	288 (8)	262 (8)	245 (8)
	Female mean (n)	256 (19)	273 (12)	278 (3)	258 (3)	247 (5)
Hemoglobin (grams %)	Mean±SE	8.9±0.32	9.8±0.37	9.9±0.57	11.2±0.60	10.6±0.67
	(n)	(21)	(18)	(11)	(11)	(12)
	Range	6.5–11.5	6.6–12.2	5.6–11.8	6.4–13.7	5.4–13.5
	Male mean (n)	9.3 (9)	10.3 (10)	9.8 (8)	11.5 (8)	10.8 (7)
	Female mean (n)	8.6 (12)	9.1 (8)	10.1 (3)	10.5 (3)	10.2 (5)
Muscle Glycogen (% wt wt)	Mean±SE	0.12±0.018	0.04±0.008	0.02±0.007	0.03±0.013	0.04±0.010
	(n)	(21)	(23)	(11)	(11)	(12)
	Range	0.05–0.31	0.001–0.12	0.001–0.07	0.001–0.13	0.002–0.11
	Male mean (n)	0.09 (8)	0.04 (15)	0.03 (8)	0.04 (8)	0.05 (8)
	Female mean (n)	0.14 (13)	0.03 (8)	0.01 (3)	0.01 (3)	0.02 (4)
Liver Glycogen (% wet wt)	Mean±SE	3.36±0.484	3.57±0.332	2.97±0.746	4.08±0.668	3.57±0.457
	(n)	(21)	(23)	(11)	(11)	(13)
	Range	0.29–7.79	0.49–6.44	0.51–8.73	0.40–7.69	1.37–7.21
	Male mean (n)	2.48 (8)	3.53 (15)	3.40 (8)	4.42 (8)	4.02 (8)
	Female mean (n)	3.91 (13)	3.65 (8)	1.81 (3)	3.15 (3)	2.85 (5)
Muscle Pyruvate (mg/100 g)	Mean±SE	3.47±0.192	6.23±0.324	6.58±0.376	5.42±0.437	4.23±0.440
	(n)	(21)	(23)	(11)	(11)	(13)
	Range	1.75–5.99	2.64–8.65	3.88–8.08	2.89–7.46	1.21–6.03
	Male mean (n)	3.67 (8)	6.10 (15)	6.79 (8)	5.18 (8)	3.84 (8)
	Female mean (n)	3.35 (13)	6.48 (8)	6.03 (3)	6.07 (3)	4.86 (5)
Blood Pyruvate (mg %)	Mean±SE	0.50±0.036	0.50±0.032	0.75±0.065	0.71±0.039	0.65±0.051
	(n)	(10)	(19)	(11)	(11)	(13)
	Range	0.36–0.67	0.29–0.79	0.53–1.21	0.54–0.93	0.40–1.06
	Male mean (n)	0.49 (4)	0.53 (10)	0.74 (8)	0.68 (8)	0.60 (8)
	Female mean (n)	0.50 (6)	0.47 (9)	0.79 (3)	0.81 (3)	0.72 (5)
Muscle Lactate (mg/100 g)	Mean±SE	187±12.5	378±18.2	426±20.2	405±13.7	415±20.4
	(n)	(19)	(23)	(11)	(11)	(13)
	Range	92–283	188–509	311–525	332–493	272–523
	Male mean (n)	197 (7)	352 (15)	438 (8)	407 (8)	403 (8)
	Female mean (n)	181 (12)	428 (6)	392 (3)	400 (3)	436 (5)
Blood Lactate (mg %)	Mean±SE	8.8±2.03	26.2±1.04	49.5±2.66	59.3±3.55	77.9±4.81
	(n)	(10)	(19)	(11)	(11)	(13)
	Range	2.5–24.6	19.8–35.3	35.1–63.8	46.2–78.3	47.3–105.1
	Male mean (n)	11.0 (4)	24.0 (10)	48.9 (8)	56.4 (8)	69.6 (8)
	Female mean (n)	7.3 (6)	28.7 (9)	50.9 (3)	67.1 (3)	91.3 (5)

HEMOGLOBIN. The hemoglobin levels in 1959 were slightly lower than those recorded in 1958. The unexercised mean was 8.9 g% (Table VI). The level increased during vigorous exercise to a value of 11.2 g% at 9 min. This increase may be a reflection of osmotic changes in the blood as discussed above.

MUSCLE GLYCOGEN. The average muscle glycogen for the unexercised condition was 0.12% wet weight (Table VI). This value is half that reported above for 1958. There is no clear explanation for the difference; however, when taken together with the lactate and pyruvate values, there is an indication that the 1959 fish were in a higher state of activity before exercise than the 1958 fish. Despite this fact, the unexercised muscle glycogen in 1959 was higher than that found in 1957 (Black *et al.*, 1960) again probably due to the use of the quick-freezing technique.

During severe muscular activity the muscle glycogen fell sharply in the first 2 min to $\frac{1}{3}$ of the resting value, and declined to $\frac{1}{6}$ in the 5th min. By the end of 15 min, the value had risen again to 0.04%, or the same as that noted after 2 min strenuous activity (Fig. 5a). The rate of depletion of glycogen in the first 5 min of activity was greater in 1959 than in 1958, but the percentage of the initial resting level remaining at the time of maximum depletion was the same in both years, namely about 16%.

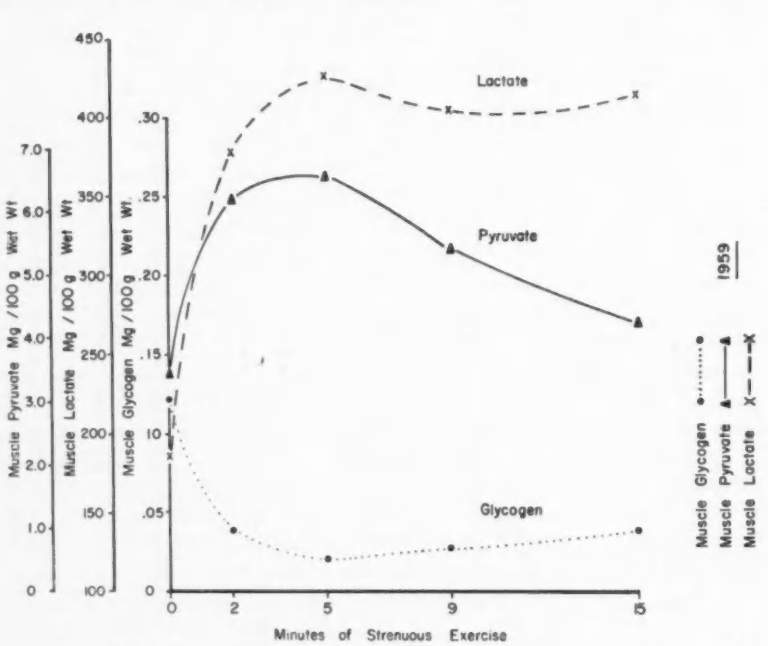


FIG. 5a. Changes in muscle levels of glycogen, pyruvate and lactate during 15 min strenuous exercise in 1½-year-old rainbow trout. 11.5°C, 1959.

The above figures are the overall average for both sexes. In females in 1959, the muscle glycogen level declined from 0.14% at rest to 0.03% after 2 min exercise and to 0.01% at the end of 5 min. In males, the initial resting value was lower than in females (0.09%), and declined during the first 2 min of vigorous activity to 0.04%. Thus the rate of depletion was considerably less in the male than the female, as was noted in 1958.

LIVER GLYCOGEN. The liver glycogen for resting fish was 3.36% wet weight (Table VI). This value is nearly 4 times the resting level reported for the 1958 rainbow trout. As was noted in 1958, the liver glycogen did not differ significantly between males and females, nor was it apparently related to the duration of muscular exercise.

MUSCLE PYRUVATE. The initial muscle pyruvate level in the 1959 trout was 3.47 mg/100 g wet tissue (Table VI). This value is more than 3 times that found in 1958. The difference is probably due in part to the use of different methods of tissue grinding (see section on Comparison of Methods); however, as noted above, there is a possibility that the 1959 fish were quite active in the unexercised state.

The increase in muscle pyruvate in the first 2 to 5 min of strenuous exercise in 1959 was 2-fold. This was less than the degree of change noted in 1958, however, the absolute levels attained in this period were nearly the same in the two years. As in 1958, the peak of muscle pyruvate production occurred at 5 min, and by the end of 15 min the value had diminished to approximately the same level in both years (Fig. 1a and 5a).

There was no significant difference between males and females in the muscle pyruvate response to exercise in 1959.

BLOOD PYRUVATE. The resting level of blood pyruvate was 0.50 mg% (Table VI), or nearly twice that found in the 1958 rainbow trout. The higher level in 1959 is another indication of greater activity in the 1959 trout.

Blood pyruvate in the 1959 fish increased 1½-fold during the first 2 to 5 min of severe muscular activity. At the end of 15 min, the value had dropped to 0.65 mg% (Fig. 5b).

There was no significant difference between males and females in the results obtained in 1959 for the various conditions.

The rate of transfer of pyruvate from muscle to blood was slower in 1959 than in 1958. The blood pyruvate did not begin to rise until after 2 min of vigorous exercise (Fig. 5b). This delay could presumably be due to the high initial level of pyruvate in the blood of resting fish in the 1959 sample.

MUSCLE LACTATE. Muscle lactate in the resting condition was 187 mg/100 g wet tissue (Table VI). This value is nearly 3 times that noted for the same condition in the 1958 experiments. As noted earlier, the higher value is probably due in large part to the use of a mechanical grinding method in 1959, however, it may also be due in part to the overall appearance of a higher level of activity in the 1959 fish.

During vigorous activity, the muscle lactate doubled in the first 2 min, and increased to a level 2½ times the resting value in 15 min (Table VI, Fig. 5a).

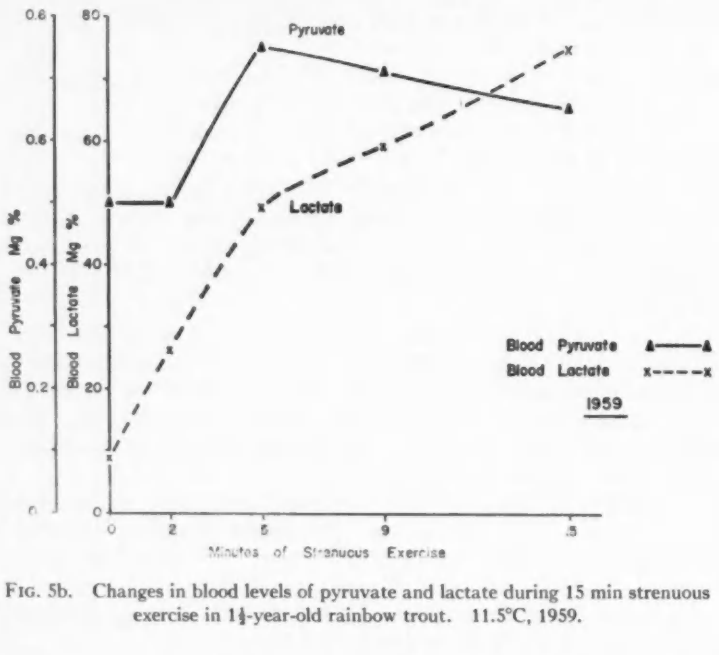


FIG. 5b. Changes in blood levels of pyruvate and lactate during 15 min strenuous exercise in 1½-year-old rainbow trout. 11.5°C, 1959.

There was no significant difference between the muscle lactate values for males and females in any of the various conditions.

BLOOD LACTATE. The blood lactate in the unexercised condition was 8.8 mg% (Table VI). This value is more than double that found in 1958, and approximates the levels found in 1957 in 1½-year-old rainbow and spawning Kamloops trout (Black *et al.*, 1960), and in 2-year-old Kamloops trout (Black, 1957a).

During vigorous activity, the blood lactate increased 3-fold in the first 2 min and more than 8-fold in 15 min (Table VI, Fig. 5b). The level at the end of 15 min was 77.9 mg%, a value substantially higher than that noted in 1958. The percentage of increase over the initial resting level was, however, less in 1959.

There was no consistent difference noted in the blood lactate levels in males and females in 1959.

A comparison of muscle and blood lactate in the various conditions tested reveals that there was a very rapid transfer of lactate from muscle to blood. The blood level had begun to rise within 2 min of the start of strenuous exercise. On the other hand, as was noted earlier, the equilibrium value of the muscle was much higher than that ever attained by the blood during severe muscular activity. At the end of 15 min, the muscle lactate was 415 mg/100 g whereas the blood level was only 77.9 mg% (Table VI).

GENERAL DISCUSSION

The results indicate that the metabolism of muscle glycogen in rainbow trout is extremely rapid (50% depletion of resting muscle glycogen in the first two minutes of vigorous activity), and that this metabolism probably provides most, if not all, of the energy requirements for severe muscular activity. MacLeod (1961) has shown by *in vitro* studies that the enzymatic pathways of glycolysis in salmon and trout are similar to those in mammals although there is apparently a deficiency of hexokinase in most tissues which would preclude the direct utilization of glucose. Black *et al.*, (1960) could find no relationship to indicate that blood glucose was being used as a source of energy in rainbow trout during exercise. Studies on the phosphorylases of fish muscle by Cordier and Cordier (1957) and Ono and Nagayama (1957) show that all the enzymes necessary for converting glycogen rapidly to lactic acid are present in the skeletal muscle and other tissues.

In moderate exercise, such as sustained swimming at cruising speeds, the rate of depletion of muscle glycogen is small (Table IV) or negligible (Black *et al.*, 1960). Other workers (Greene, 1921; Fontaine and Hatey, 1953; Idler and Clemens, 1959) have reported that during the spawning migration of salmonoids, when the fish are not feeding, large amounts of body protein and fat are consumed and presumably provide the major source of energy. However, as has been pointed out by Drummond and Black (1960), these findings do not preclude the possibility that the immediate source of fuel at the cellular level, particularly for bursts of strenuous activity such as ascending waterfalls or escaping predators, may still be muscle glycogen. The metabolism of protein and fat is essentially a slow process, hardly rapid enough for sudden spurts of muscular contraction. It has long been known that in mammals the process of gluconeogenesis provides for the formation of carbohydrate from amino acid and fat precursors (Janney and Csonka, 1915; Lusk, 1928), and the existence of a similar pathway in fish is more than likely.

The breakdown of muscle glycogen during exercise in trout proceeds through the intermediate pyruvate to the formation of vast quantities of lactate in muscle as evidenced by the markedly increased levels of both these compounds during and after exercise (Fig. 1a, 5a; Tables IV, V, VI). During strenuous exercise the level of pyruvate in muscle increases more rapidly than that of lactate in the early stages, and then begins to decline as the lactate continues to rise (Fig. 1a, 5a), indicating that lactate is being formed from pyruvate.

The blood levels of lactate and pyruvate during exercise reflect the muscle concentrations. The diffusion of these substances from muscle to blood occurs within the first few minutes of exercise although the rate of diffusion of pyruvate appears to be slower than that of lactate (Fig. 1b, 5b). Huckabee (1956) found that, in human blood cells, lactate appeared to move passively and freely across the membrane whereas the movement of pyruvate resulted from metabolic activity of the cells as well as a passive diffusion through a membrane of relatively high resistance. It is quite probable that such a difference in permeability and

manner of diffusion may exist between the muscle fibres and the extracellular fluid in trout.

During recovery from severe exercise, one of the most significant quantitative differences between the carbohydrate metabolism of fish and that of mammals becomes apparent — that is, the prolonged elevation of the blood lactate level following exercise (Fig. 4). In man, even without previous physical training the blood lactate may continue to rise for a few minutes following exercise, but drops very rapidly thereafter and usually reaches the resting level within 1 hour (Bang, 1936; Crescitelli and Taylor, 1944). In fish, however, the blood lactate continues to rise sharply for up to 4 hours following severe exercise and declines slowly, seldom reaching the pre-exercise level until the 8th-12th hour of recovery (Fig. 4; and Black, 1957a,b,c; Black *et al.*, 1959, 1960). The results presented here show that the prolonged elevation of the blood lactate is a reflection of the very slow removal of lactate from muscle (Fig. 4), and that the high lactate levels in muscle and blood are accompanied by marked elevations of the pyruvate level (Fig. 3).

It should be noted that although pyruvate concentrations in muscle and blood show marked increases during and following exercise in trout, and these increases are coincident with a depletion of muscle glycogen, it cannot be assumed that all the pyruvate comes from muscle glycogen. Under normal circumstances, the body pool of pyruvate is in a constant state of flux. Pyruvate is constantly being formed from the breakdown of amino acids and fats as well as various carbohydrates, and is continuously entering into other reactions. The levels of pyruvate should be regarded not as static entities, as has been the tendency in this discussion for purposes of simplicity, but rather as the delicate equilibrium value obtaining at the time of sampling in what is actually a dynamic system. It is reasonable, however, to assume that the major portion of the increase in pyruvate levels noted during and following exercise results from the increased rate of metabolism of glycogen under these conditions.

The metabolic reaction resulting in the formation of lactate from pyruvate requires the enzyme lactic acid dehydrogenase (LDH), and the coenzyme reduced diphosphopyridine nucleotide ($DPN.H_2$). This reaction is reversible:

$$\text{Pyruvate} + DPN.H_2 \underset{\text{LDH}}{\rightleftharpoons} \text{Lactate} + DPN \qquad \text{Formula (1)}$$

and may be expressed in its mass action form after the manner of Huckabee (1958):

$$[\text{Lactate}] = [\text{Pyruvate}] \times K\frac{[DPN.H_2]}{[DPN]} \qquad \text{Formula (2)}$$

This equation shows that the concentration of lactate is dependent on two factors, namely, the concentration of pyruvate, and the factor $K\frac{[DPN.H_2]}{[DPN]}$. The transformation of $DPN.H_2$ to DPN which accompanies the formation of lactate provides a means for the elimination of hydrogen ions (oxidation) in the absence of oxygen, and the DPN thus formed is free to re-enter the glycolytic cycle as a coenzyme in the oxidation of 3-phosphoglyceraldehyde to 1, 3-diphosphoglyceric

acid so that the breakdown of glycogen to yield energy may continue. If tissue oxygenation is adequate, pyruvate enters the tricarboxylic acid cycle and is eventually completely oxidized to CO_2 and H_2O. The reduced DPN is oxidized via the cytochrome system. In this case, a large portion of the lactate formed during the early anaerobic stages of glycolysis would be rapidly reformed into pyruvate once exercise ceases, because of the mass action effect, and oxidized via the Krebs cycle. Lactate may also be removed from the circulation by excretion or by its conversion to glycogen in the liver. Large amounts of lactate, such as were found in these experiments, are not likely to persist unless the tissue oxygenation level is low and the ratio of $DPN.H_2$ to DPN is high. It therefore seems logical to assume that during, and for several hours following, severe exercise in trout the level of tissue oxygenation is insufficient to provide for complete aerobic oxidation of carbohydrate substrates, notably glycogen.

Huckabee (1958) has suggested a formula for calculating the "excess lactate", or lactate formed in excess of the increase in pyruvate concentration and presumably due to the high value of $K\frac{[DPN.H_2]}{[DPN]}$ in formula (2).[4] When this calculation was applied to the present data and the results plotted, it was found that the "excess lactate" accounted for from 66 to 87% of the total blood lactate during severe exercise and recovery (Fig. 6a, b, c). The "excess lactate" did not begin to decline until between the 8th and 12th hours of recovery. On the other hand, during 30 min of moderate exercise, the "excess lactate" produced was only 44% of the total blood lactate.

The excretion of lactate has not been studied in fishes, however it is probably a fairly slow process. Diffusion rates are probably slower at the relatively low temperatures encountered in fish than they would be at the normal of 37°C in mammals. However, as has been demonstrated here, the transfer of lactate from muscle to blood occurs very rapidly during exercise. Therefore, the difference in diffusion rate due to temperature alone is unlikely to be a major factor in the slow removal of that substance from the muscles and blood of fish as was postulated in earlier papers (Black, 1957a, 1958; Black *et al.*, 1959). There is, however, another physical factor which may have more importance. It was noted earlier that there was consistent indication of a reduction in circulatory efficiency following severe exercise. This observation has recently been borne out by direct measurement of the distribution of injected 4-aminoantipyrine in trout under various conditions. Circulation has been shown to be considerably impaired during and following strenuous exercise (Hayashi, 1961). Diminution in circulatory efficiency would be expected among other

[4] $XL = (L_n - L_0) - (P_n - P_0)\ (L_0/P_0)$

where:

XL = excess lactate

L_0 = concentration of lactate at rest, in mM/l

L_n = concentration of lactate at time *n*, in mM/l

P_0 = concentration of pyruvate at rest, in mM/l

P_n = concentration of lactate at time *n*, in mM/l

Derivation of this formula is given by Huckabee (1958, pp. 252–253).

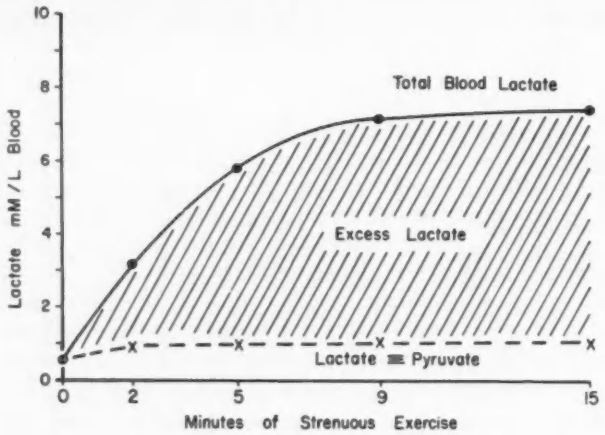


FIG. 6a. The accumulation of "excess lactate" during 15 min strenuous exercise in 1½-year-old rainbow trout. 11.5°C, 1958. The "excess lactate" is that portion of the increase in total blood lactate which is not accounted for by the increase in pyruvate.

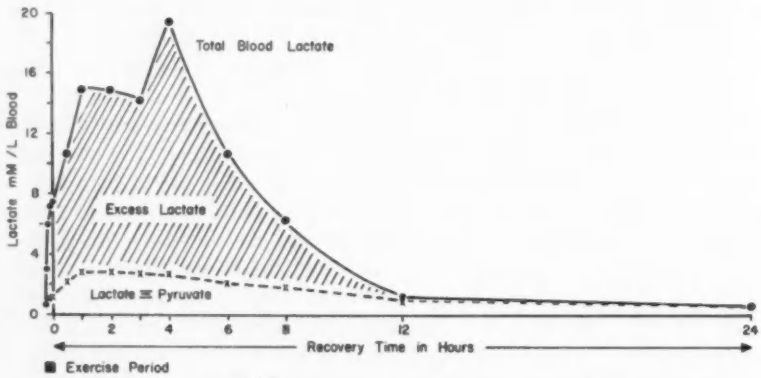


FIG. 6b. The accumulation of "excess lactate" during 15 min strenuous exercise and 24 hours recovery in 1½-year-old rainbow trout. 11.5°C, 1958. The "excess lactate" is that portion of the increase in total blood lactate which is not accounted for by the increase in pyruvate.

things to retard the removal of lactate from muscle to blood, and to interfere with the functioning of the excretory organs, gill and kidney. It is possible that the high concentration of lactate in the blood is in itself a contributing factor in the circulatory shutdown. Any study of lactate excretion in fish should be correlated with the studies of circulatory changes following exercise.

The theory was formerly widely held that lactate in mammals was rapidly removed from the blood stream by its conversion to glycogen in the liver. However, Drury and Wick (1956) have shown by the use of radioactive tagged

lactate that the amount of the naturally-occurring L(+) isomer converted to glycogen in the liver of rabbits is actually very small. The major portion is oxidized to CO_2 and water in the extra-hepatic tissues, presumably via pyruvate and the Krebs cycle. This utilization of lactate would provide a source of readily available energy. Although the results of our analyses on liver are difficult to interpret owing to the variability of individual data, there is no evidence that glycogen is being deposited in the liver during the period in which lactate is being removed from the blood stream.

It may be assumed then that while part of the lactate produced during exercise is slowly excreted, part may be oxidized and provide a source of energy during the recovery period. This theory receives further support from the observation that muscle glycogen is not restored to its initial level for a considerable period of time. Even at the end of 24 hours of recovery, the muscle

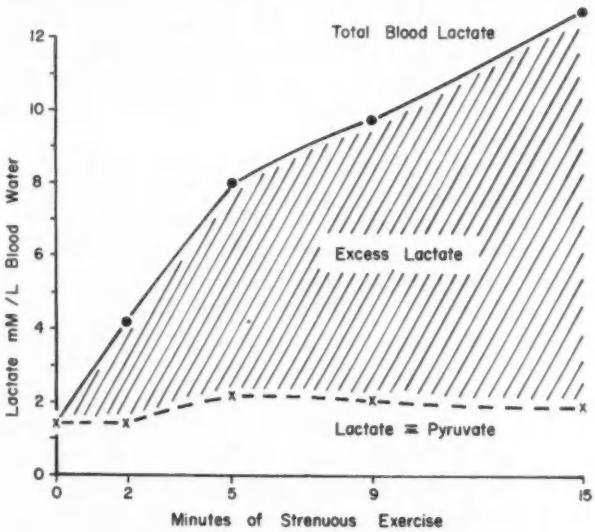


FIG. 6c. The accumulation of "excess lactate" during 15 min strenuous exercise in 1½-year-old rainbow trout. 11.5°C, 1959. The "excess lactate" is that portion of the increase in total blood lactate which is not accounted for by the increase in pyruvate.

glycogen is still one-half or less of its pre-exercise level (Table V). It appears that replenishment of glycogen in both muscle and liver after exercise is dependent on the absorption of food-stuffs from the alimentary tract (Black *et al.*, 1960), or on conversion from protein and fat stores as in the case of migrating salmonoids (Chang and Idler, 1960). The source of energy during at least part of the recovery period could well be the utilization of circulating lactate. However, this oxidation is probably fairly slow owing to the implied deficit in tissue oxygen. The low level of tissue oxygen may be attributed to several factors, namely: the impaired circulation, the low environmental oxygen tension coupled with

the relative inefficiency of the respiratory mechanism in fish, and the known fact that high levels of lactate will reduce the oxygen-combining power of hemoglobin in fish blood (von Buddenbrock, 1938; Secondat, 1950; Black, 1958). These factors, together with the problem of excretion of lactate, require further study, and may provide an explanation for the persistence of high lactate levels following exercise in fish.

In this connection, it may be postulated that the high rate of mortality noted in certain species of fish (von Buddenbrock 1938; Secondat and Diaz, 1942; Black, 1957c; Parker and Black, 1959) following severe exertion may be due to a lack of available tissue oxygen for the production of energy from lactate as well as to the deleterious effects of high lactate levels *per se* (Black, 1958).

SUMMARY

1. Experiments were carried out on water content of muscle and whole blood during vigorous exercise. No detectable changes occurred in muscle. The water content of whole blood decreased 3% following 15 min severe exercise. This decrease is in itself insufficient to account for an impairment of circulation.
2. The hemoglobin values averaged 10.2 g% in 1959 and 8.9 g% in 1959 in the resting condition. These averages are lower than those described in earlier papers. A slight but consistent rise in hemoglobin levels was noted during severe exercise and may be a reflection of the osmotic changes in blood.
3. The average muscle glycogen level in the resting condition was 0.25% wet weight in 1958 and 0.12% in 1959. Both these values are higher than those reported earlier, probably due to the fact that better sampling methods were in use.
4. The average muscle glycogen level in fish severely exercised for 15 min was 0.04% in both years. This value is lower than those reported earlier.
5. The average muscle glycogen value for 30 min moderate exercise (steady state) was 0.12%. This value is lower than those reported earlier. The lower value may have been due to the use of fish too large for the rotating chamber.
6. In 1958, the muscle glycogen decreased to half the resting value in the first 2 min of severe activity, and in 1959 to one-third in the same period.
7. The recovery of muscle glycogen following severe exercise was studied in 1958. The level rose to one-third of the resting value after 30 min recovery and, despite considerable variation, remained at approximately the same value for 24 hrs.
8. The liver glycogen levels were 4 times higher in 1959 than in 1958. No significant changes occurred in liver glycogen during activity or recovery.
9. The average resting levels of muscle pyruvate were 0.91 mg/100 g wet weight in 1958 and 3.47 mg/100 g in 1959. The difference may be attributable to more efficient grinding in the laboratory preparation of tissues, or to a greater degree of activity in the unexercised fish in 1959.

10. There was a rapid elevation of the muscle pyruvate during severe exercise. The highest levels were reached after 5 min of severe exercise and averaged 5.63 mg/100 g in 1958 and 6.58 mg/100 g in 1959.
11. Muscle pyruvate levels during recovery were followed in 1958. They did not begin to decrease significantly until after the 3rd hr.
12. The muscle pyruvate increased slightly during 30 min moderate exercise to an average of 1.73 mg/100 g in 1958.
13. The average resting levels of blood pyruvate were 0.29 mg% in 1958 and 0.50 mg% in 1959.
14. The blood pyruvate began to rise within 2 min of the commencement of severe exercise in 1958 and within 5 min in 1959. Peak levels during exercise were achieved at 9 min in 1958 (0.55 mg%) and 5 min in 1959 (0.75 mg%).
15. During recovery from 15 min severe activity, the blood pyruvate continued to rise for 1 hr reaching a level of 1.54 mg%, and then declined slowly. The resting level was not attained until 24 hrs of recovery.
16. There was a 2-fold increase in blood pyruvate during 30 min moderate exercise in 1958.
17. The resting level of liver pyruvate averaged 0.56 mg/100 g in 1958. During exercise the liver pyruvate fluctuated widely, and during recovery the level remained higher than the resting level for 24 hrs.
18. The average resting muscle lactate level for 1958 was 66 mg/100 g wet tissue, and for 1959 was 187 mg/100 g. The difference was again probably due either to the use of a more efficient grinding method or to a greater degree of activity in 1959.
19. Muscle lactate increased 3½-fold in the first 2 min of severe exercise in 1958, and doubled during the same period in 1959. Differences in rate of increase may be due in part to the higher initial level in 1959.
20. Muscle lactate levels reached 295 mg/100 g after 15 min severe exercise in 1958 and 415 mg/100 g in 1959. Muscle lactate began to decline slowly upon cessation of exercise and reached the resting level by 8 hrs.
21. Muscle lactate level after 30 min moderate exercise in 1958 was 84 mg/100 g.
22. The average resting levels of blood lactate were 4.0 mg% in 1958 and 8.8 mg% in 1959. The changes in blood lactate during exercise and recovery were similar to those reported earlier, namely, a rapid increase continuing until the 1st hr of recovery followed by a gradual decline. The resting level was approached by the end of the 12th hr of recovery.
23. The transfer of lactate from muscle to blood was more rapid than that of pyruvate. A rising blood lactate level appeared within the first 2 min of strenuous exercise.
24. The blood lactate level after 30 min moderate exercise was 13.5 mg%.
25. The resting level of liver lactate was 19.7 mg/100 g. The changes in liver lactate during exercise and recovery paralleled the changes in blood levels.

26. In 1958, a lower resting level of muscle glycogen and higher resting levels of muscle and blood lactate and pyruvate were observed in female fish as compared to male fish. The females also showed a more rapid rate and greater degree of breakdown of muscle glycogen and of accumulation of pyruvate and lactate than did the males. In the larger fish used in 1959, these differences between male and female were not evident.
27. During muscular exercise in rainbow trout, glycogen within the muscle breaks down rapidly with rapid increases in pyruvate and lactate. These changes appear concordant with those demonstrated by other workers for frog and mammal.
28. During recovery following severe exercise in trout, lactate persists in great excess over pyruvate, and muscle glycogen resynthesizes very slowly and incompletely. These changes appear to differ, in time relationship at least, from the pattern demonstrated in mammals.
29. The failure of lactate to disappear quickly from trout muscle following severe muscular activity may be due to a failure in circulation to provide oxygen and/or to provide for the removal of lactate to other organs such as the liver or excretory organs, gill and kidney. Presumably, in the lack of evidence otherwise, there may be slow combustion of the excess lactate within the muscles themselves.

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Enumeration of Coliform Bacteria in Light Salted Fish Brines[1]

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ABSTRACT

For the enumeration of the coliform bacteria present in light salted fish brines, the most probable number (MPN) procedure has been applied. Results have shown that lactose fermentation is inhibited when the inoculation of brine aliquots into plain lactose broth produces a final NaCl concentration higher than 3%. Thus erroneous low counts are obtained. It was found that this inhibitory effect could be obviated by diluting commercial fish brines with an equal volume of sterile distilled water before inoculation. The total number of coliform bacteria was determined in a number of brine samples collected at three different fish processing plants. The recommended dilution has resulted in an average 40-fold increase in total counts. All the samples collected contained significant numbers of coliform bacteria indicative of faecal contamination.

INTRODUCTION

The presence of coliform bacteria in commercial brines has been evidenced previously by various investigators. Recently Buttiaux (1958), Patton (1958) and Leistner (1958) have reported that brines from the curing of ham and bacon have constantly shown the presence of faecal *Escherichia coli* in several commercial samples examined. Although several authors agree that multiplication of coliform bacteria does not occur at NaCl concentrations higher than 10% (Hof, 1935; Garrard and Lochhead, 1939; Buttiaux, 1958), continued survival is possible under conditions of high NaCl environment, even in saturated brines (Tanner, 1919; Kenyoun, 1925; Reeves and Harrison, 1957). Consequently it becomes evident that the brining of meats does not ensure destruction of coliform bacteria; it only has a selective bacteriostatic action which is conditioned by temperature and other constituents of the brines.

In reference to the presence and survival of coliform bacteria in fish brines, a very limited amount of literature appears to be available. Frank and Hess (1941) reported the survival of both *E. coli* and *Eberthella typhosa* after prolonged exposure to high NaCl concentrations. More recently Bain *et al.* (1958) reported that *E. coli* type I can remain viable in both fresh and used fish brines for at least 8 days at 15°C.

For various reasons, the reliability of coliform bacteria as an index of faecal contamination has been disputed. However, the examination of several hundreds of commercial brines has permitted Buttiaux and Moriamez (1958) to conclude that *E. coli* is a reliable index for detecting faecal contamination and that it is

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even better than faecal streptococci for the examination of young meat brines less than 8 days old. Also, Frank and Hess (1941) found that the presence of coliform bacteria on salt fish could be used as a measure of sanitary control.

In order to evaluate the possible use of the standard coliform test as an index of sanitary control in light salted fish brines and to obtain an idea of the present hygienic conditions, representative samples of brine obtained from commercial curing establishments have been examined.

MATERIAL AND METHODS

The brines from light salted fish of the Gaspé-cure type are different from the cover brines normally prepared for the curing of meats such as beef, bacon and ham. They are formed by the addition of dry salt to split codfish in vats. The salt is added in the proportion of about 7 to 9 lb to a 100-lb lot of fish and, usually after 24 hours, sufficient brine is formed by osmosis to cover the fish as it is weighted down with a heavy stone.

Samples of brine were taken during the months of July and August at three different fish processing plants referred to as plants A, B and C for the purpose of concealing their identity. These samples were collected in sterile containers immediately after the fish had been removed from the salting vats, which is usually 3 to 4 days after the beginning of curing. The brines were vigorously swirled in the vats several times to ensure a thorough mixing. The samples were brought to the laboratory for analysis within one hour after collection.

The salt content was determined by the silver nitrate titration method of Dyer (1943). In the data referring to preparation of culture media "% NaCl" refers to the number of grams of NaCl added to 100 ml broth. Coliform bacteria were enumerated according to a standard "most probable number" (MPN) procedure (APHA, 1955), using plain lactose broth as culture medium and five replicate tubes each for the following portions of samples: 10, 1.0 and 0.1 ml. The presence of coliform bacteria was confirmed on Eosin–Methylene Blue Agar plates. Isolation of coliform strains was performed by serial dilutions plated on nutrient agar and further differentiation was obtained by the IMViC procedure (=indol, methyl red, Voges–Proskauer and citrate tests).

Lactose fermentation was evaluated by the gas production in Durham tubes after 48 hours at 37°C. Occasionally Smith tubes were used. Tubes showing more than 10% gas were considered positive. In other experiments, CO_2 was measured quantitatively according to an adaptation of the procedure described by Van Slyke *et al.* (1941).

Growth was estimated by turbidity measurements of broth cultures using the Beckman Model C colorimeter at 440 mμ.

RESULTS AND DISCUSSION

Preliminary Observations

During the initial stages of the survey on the presence of coliform bacteria in commercial brines one notable observation was repeatedly made. More positive lactose tubes were always obtained from the 1-ml inoculated portions

of brines than from the 10-ml portions. One typical example of such abnormal results obtained in terms of MPN is as follows:

For the 10-ml inoculated portions — 1 positive out of 5 tubes
For the 1-ml inoculated portions — 5 positive out of 5 tubes
For the 0.1-ml inoculated portions — 2 positive out of 5 tubes.

In some extreme cases, brines giving fully positive results (5/5) with the 1-ml portions showed totally negative results (0/5) with the 10-ml portions of brine.

From such preliminary observations it was felt that these abnormal results might be caused by the presence of excessive NaCl content in the inoculated lactose broth. Using the MPN technique, this would mainly occur with the larger inocula, because by adding 10-ml portions of brine to 20 ml of lactose broth the NaCl concentration becomes one third that of the original brine. Thus it would seem that the final NaCl concentration in the large lactose tubes would be sufficiently high to inhibit gas production from lactose.

Effect of Brine Dilution

An attempt was made to determine the effect of brine dilution on the total number of coliform bacteria. The NaCl concentration of 28 commercial brines obtained from the preparation of light salted fish was determined and found to vary between 13.0 and 17.0%.

Sterile distilled water was added to the brines in varying amounts in order to obtain a series of gradual dilutions. Each one of these dilutions was inoculated into tubes of lactose broth for determining the MPN of coliform bacteria. Replicate experiments have yielded results of identical order and Table I summarizes those obtained from a typical commercial brine containing 15.8% NaCl.

Table I. Effect of brine dilution on NaCl concentration and on total count of coliform bacteria.

Dilution	% NaCl		Proportion of positive tubes			MPN	
Brine : H_2O	In brine	In large lactose tubes	10-ml	1-ml	0.1-ml	Diluted	Corrected
1 : 0.0	15.80	5.27	1/5	5/5	3/5	19	19
1 : 0.5	10.53	3.51	4/5	5/5	2/5	56	84
1 : 1.0	7.90	2.63	5/5	4/5	1/5	170	340
1 : 1.5	6.32	2.11	5/5	3/5	1/5	110	275
1 : 2.0	5.27	1.76	5/5	3/5	0/5	79	237

The results reported in Table I again clearly indicate that undiluted or weakly diluted brines produce fewer positive lactose tubes with the large portions of inoculated brine than with the smaller portions. Consequently the total counts obtained from undiluted brines are erroneously low: they represent only 5.6% of those obtained when they are properly diluted. It is also shown that maximum counts are obtained when the brines are diluted 1 : 1 with distilled

water before inoculation into lactose tubes. Since the effect of high NaCl concentration only takes place in the larger lactose tubes, Table I shows the effect of dilution on the NaCl concentration in these tubes only. The optimum degree of dilution for obtaining maximum counts (1 : 1) reduces the final NaCl content to 2.63 from 5.27%. Therefore it would seem that the critical NaCl concentration affecting lactose fermentation lies close to 3%.

Effect of NaCl on Coliform Bacteria Isolated from Brines

Coliform bacteria isolated from commercial brines have been tested for their ability to grow and to ferment lactose in the presence of different concentrations of NaCl. In one set of experiments the inocula have consisted of a mixture of coliform organisms taken from a positive lactose tube and transferred into series of five lactose broth tubes containing increasing NaCl concentrations. These tubes were examined after different time intervals and the appearance of 10% or more gas in the inverted vials was considered a positive test. The results obtained are summarized in Table II and show, as in the previous experiment, that lactose fermentation by a mixed population of coliform bacteria present in commercial fish brines is inhibited by the presence of 3% NaCl.

Table II. Effect of NaCl on lactose fermentation by a mixed population of coliform bacteria from commercial brines.

	Percentage NaCl in lactose broth						
Time (hours)	0	1.0	2.0	2.5	3.0	3.5	4.0
18	5*	5	2	0	0	0	0
24	5	5	3	1	0	0	0
36	5	5	5	5	0	0	0
48	5	5	5	5	1	0	0

*Number of positive tubes from the five used.

The coliform bacteria present in commercial fish brines have been further differentiated by transfer on Eosin–Methylene Blue Agar, with isolation and confirmation via the IMViC procedure. Thus, strains of *E. coli* type I, *Aerobacter aerogenes* type II and *E. freundii* (intermediates) type II were isolated, indicating a mixed population composed of a large proportion, approximately 70%, of faecal contaminants.

In one experiment, a strain of *E. coli* isolated from fish brines has been compared with a pure *E. coli* culture obtained from stock collection for NaCl tolerance. The results obtained after incubation for 48 hours at 37°C are illustrated in Fig. 1. Although both strains show growth curves of identical features, namely stimulation in the presence of low NaCl concentrations, complete growth inhibition occurs at 6% NaCl for the stock culture and at 8% for the strain isolated from fish brines. When incubation was continued for an additional 48 hours the inhibitory NaCl concentrations were increased to 7 and 9% respectively. These data suggest that coliform bacteria acquire an increased degree of resist-

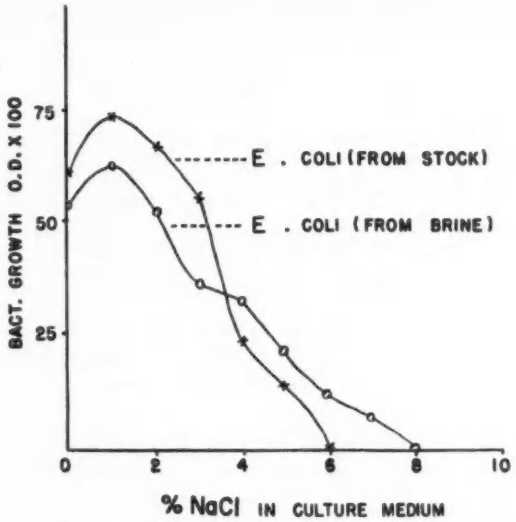

FIG. 1. Effect of NaCl on bacterial growth of *E. coli* strains from different sources.

ance from exposure to a high NaCl environment. Amongst several other authors, Reeves and Harrison (1957) have made similar observations concerning the adaptability of *E. coli* to high NaCl concentrations.

It also appears from these results that the growth of pure cultures of coliform bacteria is inhibited at a higher NaCl concentration than that causing inhibition of lactose fermentation. A clearer picture of this discrepancy has been obtained by comparing the effect of NaCl on the growth and the CO_2 production by pure coliform strains. The cultures tested were isolated from fish brines; one strain of *E. coli* type I and one strain of *Aer. aerogenes* type II. They were inoculated into lactose broth containing increasing concentrations of NaCl. Incubation at 37°C was carried out for 48 hours, the same time interval recommended for the MPN test. Bacterial growth is expressed as optical density and lactose fermentation as milligrams of CO_2 per 100 ml culture medium. Figure 2 summarizes the results obtained and shows that growth inhibition occurs at 8% NaCl for the *E. coli* strain and at 9% for the *Aer. aerogenes* strains. On the other hand, lactose fermentation stops completely at 6 and 5% NaCl respectively. It is therefore shown that lactose fermentation is inhibited at a NaCl concentration appreciably lower than that required to inhibit bacterial growth.

Previous results have shown that lactose fermentation used in the MPN test for enumerating coliform bacteria in brines was inhibited at the 3% NaCl level (Tables I and II). This limiting concentration is approximately half that shown by the pure coliform strains isolated from the fish brines. Two explanations might be offered for this difference. First, with the MPN procedure, only the tubes showing 10% or more gas are considered positive.

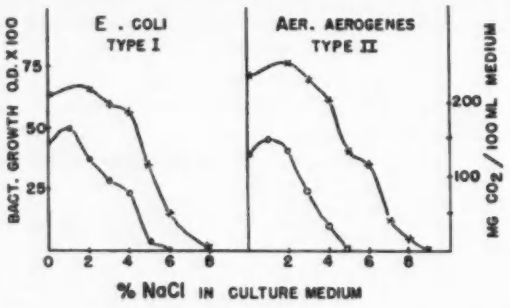

FIG. 2. Effect of NaCl on bacterial growth (× — ×) and CO_2 production (O — O) by coliform strains from light salted fish brines.

Therefore the 3% NaCl concentration does not necessarily produce complete inhibition of gas formation. Secondly, lactose fermentation by fish brines is subjected to the interaction of a large variety of microorganisms whose total counts often run as high as 1×10^9 per millilitre of brine.

EXAMINATION OF COMMERCIAL FISH BRINES

During a 2-month interval, twelve commercial brines from the preparation of light salted fish have been collected from three local plants. Immediately after collection in sterile containers they were analysed for NaCl content. Coliform bacteria were enumerated in both the undiluted and diluted (1 : 1) samples by the MPN method using plain lactose broth.

The results presented in Table III include the NaCl content of the original brines and also, on account of their special significance, the NaCl content of the large lactose broth tubes resulting from the addition of 10-ml aliquots of commercial brines, both diluted and undiluted.

For the purpose of simplification, the number of positive tubes for the three inoculated portions of brine which are normally used for establishing the MPN of coliform bacteria has not been included in Table III. However, the same observation made in the preliminary experiments was again obtained. All the samples of undiluted brine produced fewer positive tubes with the 10-ml inoculated portions than with the 1-ml and the 0.1-ml portions. Dilution of the brines completely reversed the situation and a greater number of positive tubes were obtained with the larger portions.

For all the brine samples, the addition of 10-ml portions to the large tubes of lactose broth gave a final NaCl content never lower than 4.3%; when the same samples were diluted with an equal volume of distilled water, the corresponding NaCl concentrations never exceeded 2.75%. The dilution factor of 1 : 1 seems therefore the optimum for obtaining maximum counts of coliform bacteria and for keeping the NaCl content of the inoculated portions below the 3% inhibitory level.

TABLE III. Total count (MPN) of coliform bacteria in commercial fish brines, undiluted and diluted (1 : 1).

Plant	Sample number	% NaCl in brine	Undiluted brine		Diluted brine		MPN ratio of diluted to undiluted
			% NaCl in large lactose tubes	MPN	% NaCl in large lactose tubes	MPN	
A	1	13.5	4.5	26	2.25	700	27
	2	14.0	4.7	13	2.35	260	20
	3	14.7	4.9	17	2.45	480	28
B	1	14.5	4.8	15	2.4	480	32
	2	13.0	4.3	45	2.15	1080	24
	3	15.6	5.2	45	2.6	3200	70
	4	16.4	5.5	17	2.75	700	41
	5	14.5	4.8	37	2.4	1080	29
C	1	16.1	5.4	45	2.7	1840	41
	2	15.8	5.3	13	2.65	700	54
	3	14.8	4.9	81	2.45	4800	60
	4	15.6	5.2	22	2.6	1080	50

Table III also shows that dilution of the brines produces a 20- to 70-fold increase in the total numbers of coliform bacteria, giving an average of about 40-fold. This clearly indicates the magnitude of possible error in reporting total counts of coliform bacteria in brines and the necessity of dilution in order to avoid erroneous low counts.

CONCLUSIONS

In view of the public health significance attached to the presence of coliform bacteria and particularly *E. coli* in foods as an index of potentially dangerous contamination, a good deal of attention has been paid to the occurrence of these bacteria in marine fish. According to the findings of Gibbons (1934), Griffiths (1937) and Spencer and Georgala (1958), coliform bacteria are rarely found in sea water distant from shore and *E. coli* is not a normal inhabitant of marine fishes. Griffiths and Fuller (1936) have further concluded that their presence in fish is largely due to handling after the catch.

The present study has revealed that it is possible to enumerate coliform bacteria in fish brines by the MPN procedure, providing that the NaCl content of the brine is first determined and that it is adjusted by proper dilution with distilled water to a concentration inferior to the 3% inhibitory level. The examination of several commercial brines collected at three different plants has shown that coliform bacteria are invariably present in relatively large numbers. Contamination through the use of polluted well-water, contamination through contact with dirty boats and other soiled surfaces during processing, or through direct contact with carriers, have been considered as possible sources of infection.

The accuracy of the MPN procedure might not be as great as some others, but it seems suitable for carrying out a routine examination of commercial fish

brines. When supplemented with confirmatory tests, it has shown that brines produced during the preparation of light salted fish are grossly contaminated with microorganisms of faecal origin. Even if bacteriological standards have not yet been established, in view of the fact that these bacteria survive on the final product (Frank and Hess, 1941), recommendations should be made for greater care and better hygienic conditions in fish curing establishments.

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Cod Tagging in the Newfoundland Area During 1947 and 1948[1]

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ABSTRACT

About 4200 cod were tagged in the Newfoundland and Labrador inshore areas and on the Grand Bank and St. Pierre Bank. The migrations of tagged cod are described from tagging in the inshore fishing areas off Nutak and Domino in Labrador, off Englee, St. John's, Burin and Corbin, and Lark Harbour in Newfoundland and on the Grand Bank and St. Pierre Bank. Most cod tagged in the inshore areas were recaptured close to the tagging areas with a gradual increase with time after tagging in the average minimal distance moved. There is, at least in many areas, a southward winter and a northward spring and early summer movement of cod.

The greatest number of recaptures (after the tagging year) of cod tagged inshore were in the shallow waters of the inshore area from June–September. From July to February–March recaptures were from progressively deeper water with some recaptures in the shallow inshore waters by May and many by June. Some recaptures, however, were still from deep water in June–September.

Cod caught inshore by commercial fishermen and offshore by research otter trawler were tagged, some with an external, combination cellulose nitrate and aluminum disc bachelor-button tag inserted through the opercular bone, some with a 2-inch, flat cellulose nitrate tag inserted in the body cavity through a posterior slit in the body wall. Injuries at the point of insertion of the tag were often quite severe for the external, but generally mild for the internal tags, long after the time of tagging. The internal tags gave fewer returns than the external tags in the tagging year, but the opposite was generally true for the years following. In years after the tagging year the percentage recaptures of smaller cod were greatly in excess of those of larger cod. In the year after the tagging year smaller tagged cod — those up to 60 or 70 cm — showed less significant movement than larger tagged cod. Although cod were recaptured almost immediately after being tagged from traps, those tagged from handlines and linetrawls were not caught by baited hooks for 7–10 days afterwards. An inverse relationship exists between the length of otter-trawl drag from which fish were tagged and the percentage recaptures.

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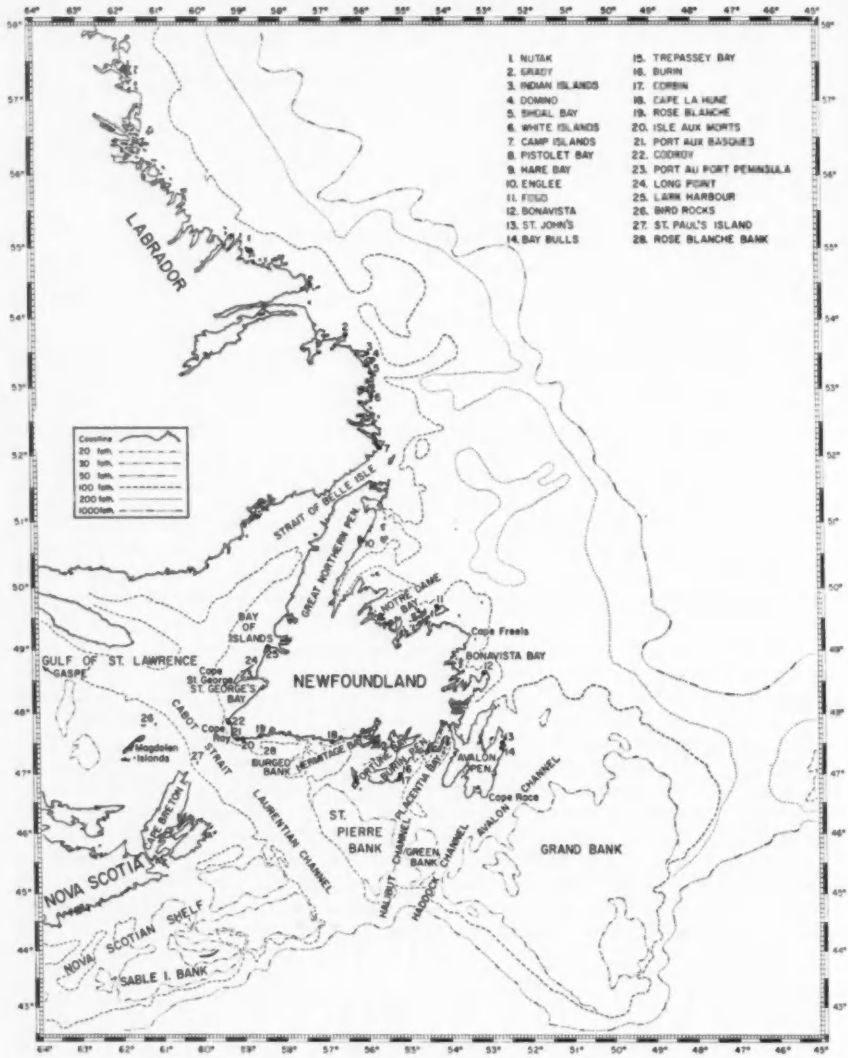

FIG. 1. Map showing location of places named in text.

INTRODUCTION

IN 1947 AND 1948 cod (*Gadus morhua* L.) of commercial size, over 40 cm long, were tagged in the Newfoundland area to obtain increased knowledge of the migrations and of the degree of distinctness of various cod stocks. In 1947 tagging was carried out at Englee on the northeast coast of Newfoundland, on

the southern parts of the Grand Bank and on St. Pierre Bank. In 1948 cod were tagged at Nutak and Domino in Labrador, at St. John's on the east coast of Newfoundland, Burin and Corbin on the south coast, near Lark Harbour, Bay of Islands on the west coast of Newfoundland, and again on Grand Bank and St. Pierre Bank (Fig. 1).

Considerable numbers of cod in the Newfoundland area had been tagged previously (8651 between 1933 and 1937) and recaptures resulting from this earlier tagging have been reported by Thompson (1943). The tagging in 1947 and 1948 was in some cases in or close to some of Thompson's tagging areas, and in other cases in new areas.

Most of the recaptures of cod shown in this paper are from the inshore area. The numbers of tagged cod returned from an area are related to the amount

FIG. 2. The distribution of the inshore catch of cod in Newfoundland, yearly average, 1947–1949. (1,000 quintals, mainly light-salted dried cod = approximately 500,000 lb or 226,800 kg fresh round cod.)

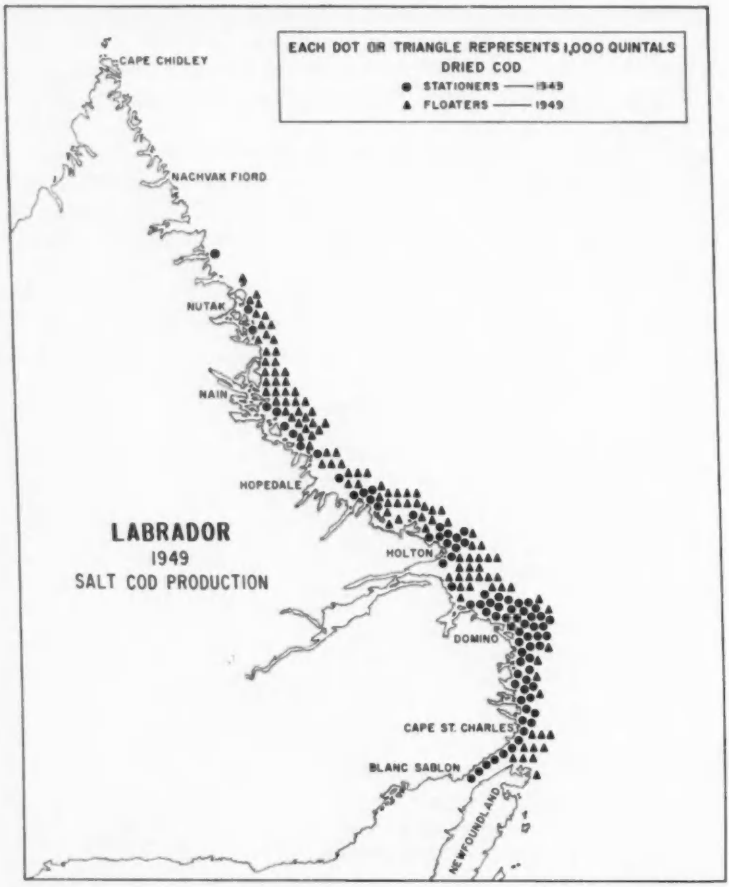

FIG. 3. Distribution of the inshore catch of cod in Labrador by stationers (shore-based fishermen) and floaters (schooner-based fishermen), 1949. (1,000 quintals Labrador cure, heavy-salted dried cod = approximately 420,000 lb or 190,500 kg fresh round cod.)

of cod caught in the commercial fishery and to the amount of fishing ground available in an area. The distribution inshore of the catch of cod in Newfoundland from 1947–1949 and in Labrador for 1949 is shown in Fig. 2 and 3; this distribution and the contributing factors have been discussed by Templeman (1958). For the offshore and bank areas, where the catch is almost entirely by European vessels, the location of distribution of the cod catch by limited areas is not available for the period covered by this tagging. However, for 1956, which is close in time to the years during which most tags were returned, the catch location by ICNAF divisions can be seen in the Statistical Bulletin of the International Commission for the Northwest Atlantic Fisheries (1958).

MATERIALS AND METHODS

In the cod tagging experiments during 1947 and 1948 two types of tags were used. The external bachelor-button tag was fastened, using specially adapted pliers, to the gill cover on the left side through a hole punched in the opercular bone with a leather-punch. The internal flat tag was inserted into the body cavity through a slit made in the body wall on the left side with a sharp scalpel. Fig. 4 illustrates both types of tags and the instruments used in tagging, and Fig. 5 shows where the tags were inserted.

The external bachelor-button or opercular tag was the same as that used by Thompson (1943) in cod tagging in the Newfoundland area and described by him as follows: "The tag employed was that used by the United States Bureau of Fisheries in marking haddock through the bony gill cover and consisted of two concave discs, one being of aluminum, and having a neck or collar, which was clamped by pliers to the other. The latter consisted of a red, laminated celluloid disc of cellulose nitrate, with a central hole and having the serial number of the tag and directions as to its return to the Laboratory." The discs were about 1.5 cm in diameter, and the tag was attached with the red celluloid disc on the outside and the metal disc on the inside of the gill cover. In punching the hole through the opercular bone prior to attaching the tag it was found necessary to lift the gill cover somewhat so that none of the filaments of the outside gill on the tagging side would be damaged by the punch. For further details concerning the bachelor-button tag and its previous use see Templeman and Pitt (MS, 1961).

The internal tag was cerise red, of laminated cellulose nitrate material, 2 inches (5.1 cm) long, $\frac{3}{8}$ inch (0.95 cm) wide and 0.035 inch (0.09 cm) thick, rounded at both ends. On one side was printed the serial number of the tag, on the other the address of the Station and instructions to the finder of the tag. To insert the tag a small slit just large enough to admit the tag was made in a position about 5 to 8 cm (depending upon the size of the fish) antero-dorsally to the vent. In all the tagging at Corbin and for 59 of the cod tagged at St. John's the slit was made dorso-ventrally, across the muscle fibres. In all other areas where internal tags were used, the slit was made antero-posteriorly, parallel to the muscle fibres. Examination of recaptured fish which had been tagged with the internal tag showed that the healing of the wound was apparently much better for fish in which the slit had been made parallel to the muscle fibres than for fish in which the slit was across the muscle fibres. In the latter case it was evident that a cut across muscle fibres caused them to contract somewhat, keeping the incision open. Care was taken in making the cut and inserting the tag not to injure the internal organs, such as liver, gonad, and stomach. In the tagging at Englee the tags, when inserted, were pushed posteriorly, but in all other areas where the internal tags were used, they were pushed anteriorly.

In the Domino, Nutak, Burin and Corbin areas fish for tagging were taken from cod traps set in 12–15 fathoms (22–27 m) of water and operated by commercial fishermen. When a trap was hauled and the fish were brought close to

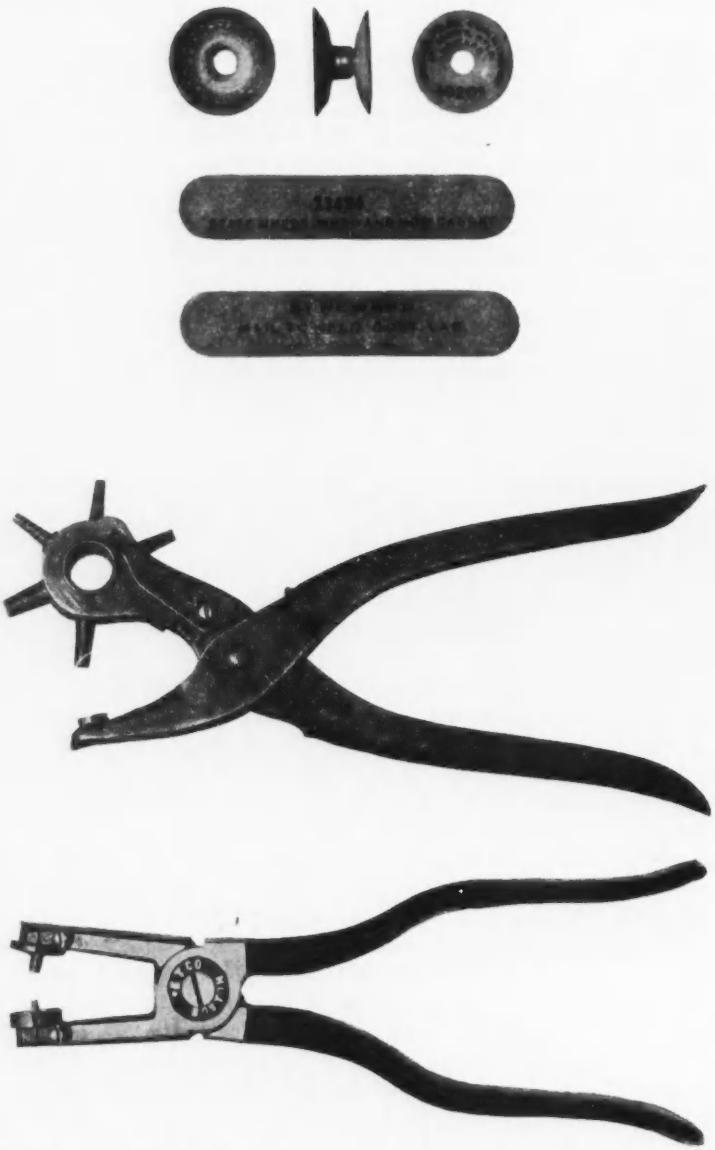

FIG. 4. Above: bachelor-button tag which was fastened externally through opercular bone, and internal tag which was inserted in body cavity through a slit in the body wall (actual size). Below: instrument for punching hole in opercular bone, and pliers for clamping the discs of the bachelor-button tag together when attaching it (half size).

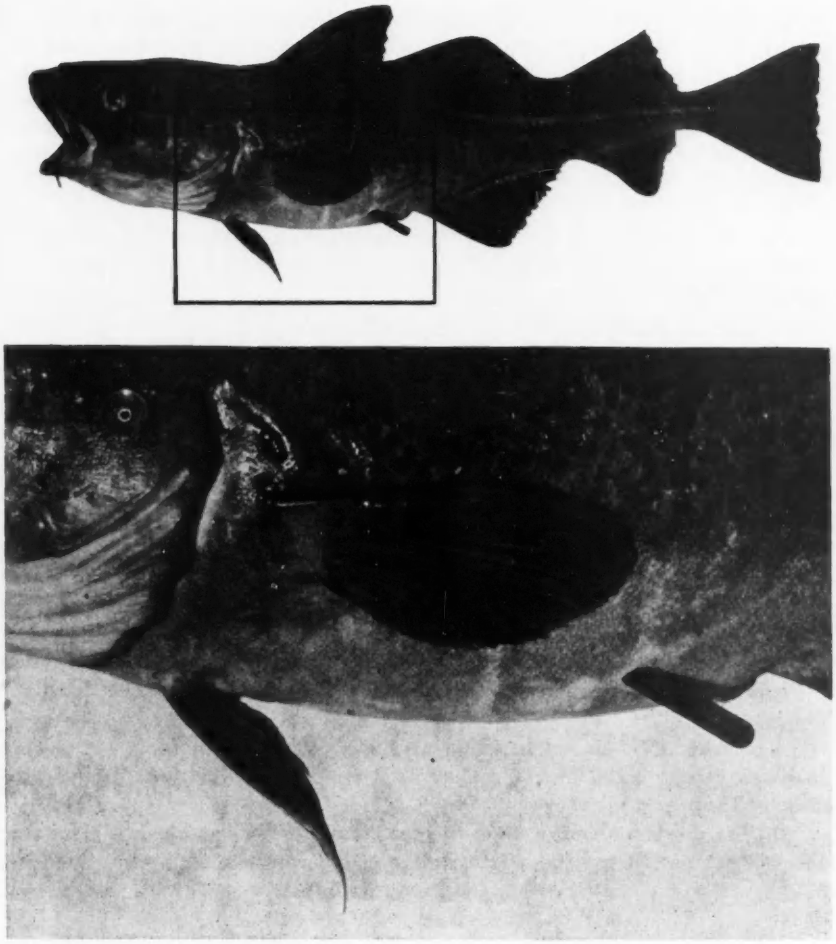

FIG. 5. Cod showing bachelor-button tag attached and internal tag partially inserted.

the surface, active ones were removed one by one as tagging proceeded, using either a dipnet or a gloved hand.

In the Domino area, where a separate boat was available for use of the tagging group, it was found useful, in order to prevent delay to the commercial fishermen, to dip about a hundred fish into a small box-trap of mesh, 6 feet square and 6 feet deep (2×2 m). This was held at the surface by the side of the tagging boat as tagging proceeded.

Fish taken by cod trap were found to be excellent for tagging, and usually could be tagged without difficulty. However, a problem can be encountered,

as shown by an extract from the tagging diary for the Nutak area on Aug. 14, 1948:

"At the tagging location near the trap the bottom temperature was 4.1°C, the surface temperature 9.5°C. The day was sunny and very warm; little wind reached us under the shelter of the high island. When we began tagging, the first few fish were very weak and several were unable to swim down. We presumed the high surface temperatures were having a lethal effect on the fish. More of the trap was now slackened to allow the trapped fish to swim deeper, and of these the more active ones were brought to the surface with a long-handled dipnet to be tagged."

Off Englee most of the fish were tagged from a commercial fisherman's linetrawls (longlines hauled by hand), one set in 40–50 fathoms (75–90 m) and the other at 50–80 fathoms (90–145 m). Off St. John's the fish for tagging were linetrawled by a commercial fisherman in depths of 30–70 fathoms (55–130 m). In addition, both off Englee and St. John's, some fish were tagged after being caught by baited handline, off Englee in 40 fathoms (75 m) and off St. John's in 25–35 fathoms (45–65 m). All fish tagged in the Lark Harbour area were handlined in depths from 17–24 fathoms (31–44 m).

When tagging from a linetrawl it was usual to haul the trawl soon after setting it, using for tagging only those fish which were alive and active, and with only superficial injuries around the mouth through being hooked on the trawl. Often a trawl was hauled several times in the one period. Most fish caught in this manner were found quite suitable for tagging, even when the trawl was baited and allowed to remain in the water overnight. The main difficulty encountered was that fish coming from the depths in which linetrawling was carried out often had the abdomen partially distended with gas. If these fish could not be deflated by applying gentle pressure to the abdominal region, they were not used for tagging.

Cod caught by baited handline were generally more suitable for tagging than fish caught on linetrawl. They were more active, and few, if any, were distended with gas.

In the tagging operation from cod trap, linetrawl or handline, as a suitable fish was removed from the water it was placed immediately on a measuring board, the length was recorded, a tag inserted or attached and the fish released in the sea. This operation required approximately 15 seconds.

For all the tagging in the Grand Bank and St. Pierre Bank areas fish were caught by the research vessel *Investigator II* using an otter trawl. Fish for tagging were generally taken from sets in depths less than 50 fathoms (90 m), though occasionally fish were tagged from depths to 80 fathoms (145 m) and once from over 90 fathoms (165 m). When cod were released from the net onto the deck of the ship a number of active, uninjured fish were placed in a large tub into which seawater was continually pumped. Fish were removed one by one from the tub, measured, tagged and returned to sea in the usual manner. The vessel was stopped while tagging proceeded.

After returning a fish to the sea an observer would check to ensure that its descent toward bottom was successful. Fish which floated up within reach were dipped back into the boat and the tags removed; if one floated up out of reach it was so recorded and not considered to be successfully tagged.

Many tagged fish recaptured in the St. John's area were brought to the Station for examination. Also, many fishermen from other areas, when returning a tag, included a description of the injury caused by the tag.

It was evident that many of the bachelor-button external tags caused serious injury in the region of attachment. At times the injury to the gill cover was such that the flesh and bone around the tag decayed and the tag fell out. About a month after the tagging period some St. John's fishermen reported seeing in their catches of cod, fish with round holes in the gill cover at the point of attachment of the bachelor-button tags.

Some of the bachelor-button tags still attached caused varying degrees of injury. In the most serious cases the skin, flesh and bone on the outside of the

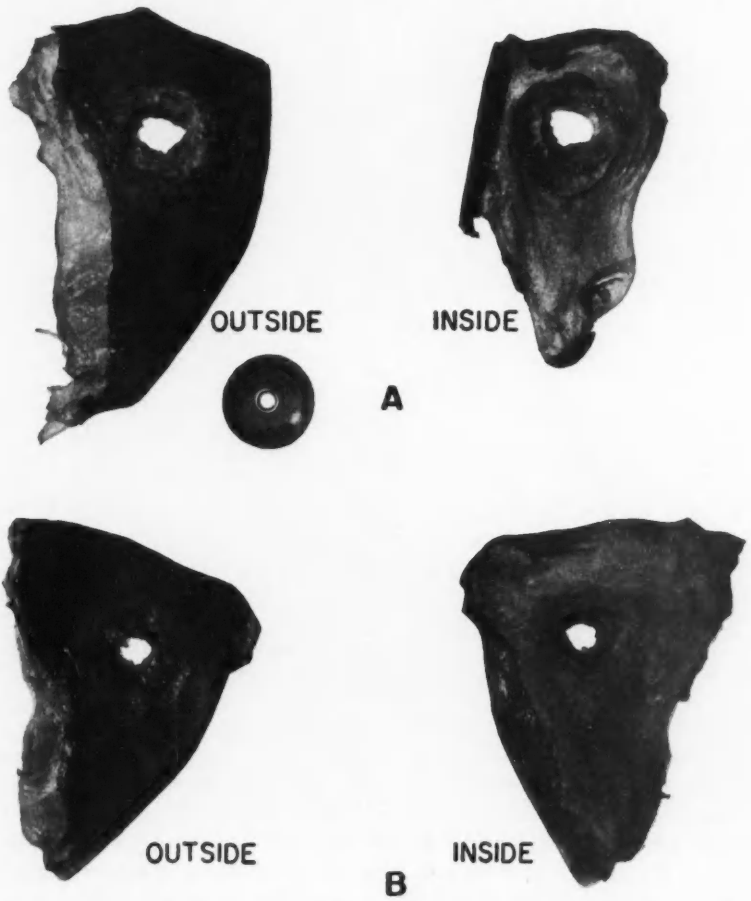

FIG. 6. Injuries to gill cover caused by bachelor-button tag. A. Serious injury, with flesh and bone badly decayed. B. Minor injury, with superficial skin abrasions, healing well advanced. (Tag disc and specimens actual size. Tags attached less than 2 months.)

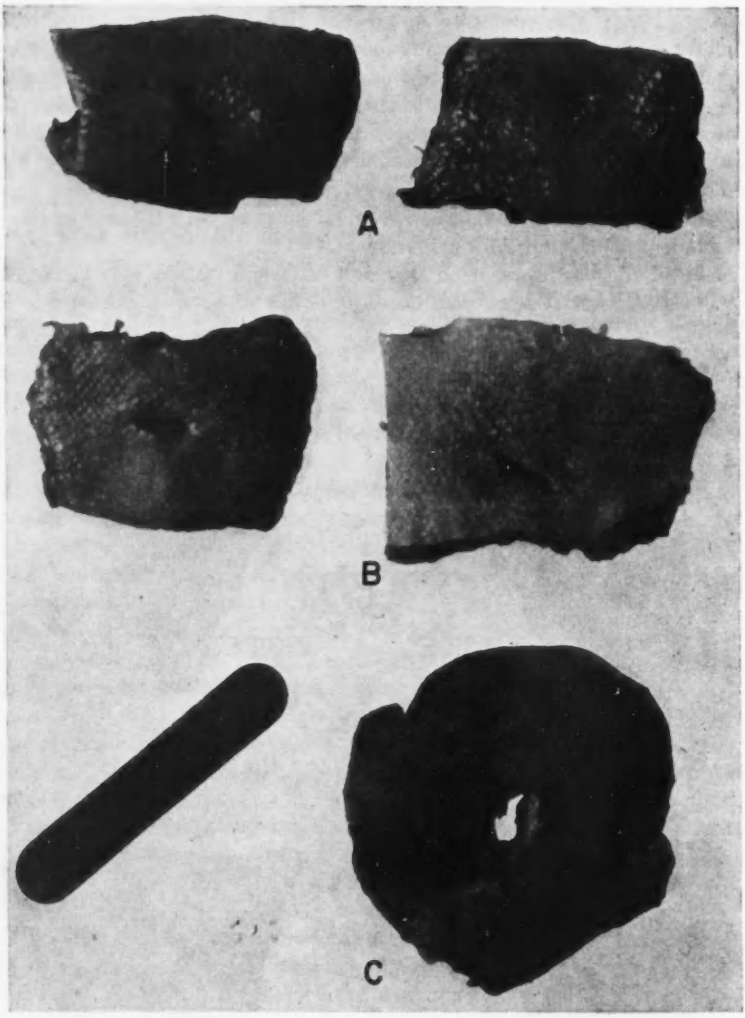

FIG. 7. Injuries at the point of insertion of the internal tag. A. Minor, incision closed, healing well advanced: left — fish free 372 days, right — fish free 44 days. B. Moderate, healing in progress, incisions not completely closed: left — 256 days free, right — 14 days free. C. Serious, incision gaping open: 11 days free. (Tag and specimens actual size.)

gill cover under the celluloid disc and on the inside of the gill cover under the aluminum disc were abraded and decaying with considerable festering and swelling of the surrounding flesh, and the hole in the bone much larger than the one originally cut (Fig. 6A). In others, though there was abrasion and bruising of skin and flesh, definite signs of healing were apparent. Finally, in some

specimens, the wound resulting from the bachelor-button tag remained uninfected, or, at the time of recapture, healing was so far advanced that injuries were of a minor nature, consisting of superficial abrasion of the skin in the region under the discs (Fig. 6B).

In addition to injuries on the inside and outside of the gill cover, in some specimens filaments of the outside left gill which came in contact with the aluminum disc were bruised and inflamed. In some specimens, also, the aluminum disc had abraded the skin over the cleithrum on the left side.

Injury caused by the slit in the body wall for insertion of the internal tag was generally of a minor nature (Fig. 7A). No serious infection was noted around the incision in any recaptured cod which had been tagged with an internal tag and returned to the Station. All showed definite signs of healing. Some cases, in which the incision was still open, were attributed to the cut in the body wall having been made obliquely (Fig. 7B, right) or across the muscle fibres (Fig. 7C), causing them to contract. As a result, the healing period was apparently prolonged. Inside the body cavity there were some instances wherein the tag was partially embedded in the liver, others where the peritoneum was either slightly torn around the incision or inflamed in the area in which the tag was lying. These injuries all appeared to be of a minor nature.

MIGRATIONS OF TAGGED COD

Nutak

Two hundred and twenty-six cod were tagged, Aug. 12–14, 1948, near the islands outside Nutak (Fig. 8). Fifteen tagged cod were recaptured in the tagging area in the month of tagging and otherwise there were only 2 recaptures, which were in the year following tagging. One showed a short migration, and one a long migration of almost 300 nautical miles (560 km) southward along the Labrador coast.

The Nutak area and the regions immediately to the north and south are sparsely inhabited and the total catch of cod from the northern Labrador was low in the years following tagging. These factors, together with the isolation of the area, are probably sufficient to account for the small number of returns.

Domino

The tagging of 505 cod in the Spotted Islands area near Domino was carried out between July 12 and 22, 1948 (Fig. 8). In the tagging year the one cod recaptured outside the general neighbourhood of tagging showed a short movement southward off Labrador. In 1949 most recaptures were still near the tagging area but there had been a short movement northward and several fish had moved southward to the northeast coast of Newfoundland. The distribution in 1950–1952 was similar to that of 1949, except that a smaller proportion of recaptures was from the immediate tagging area.

On the northeast coast of Newfoundland and off southern Labrador, cod spend the winter in deep water mostly below 100–120 fathoms (180–220 m). This deep water usually begins within 5–40 miles (8–65 km) of the coast. Though

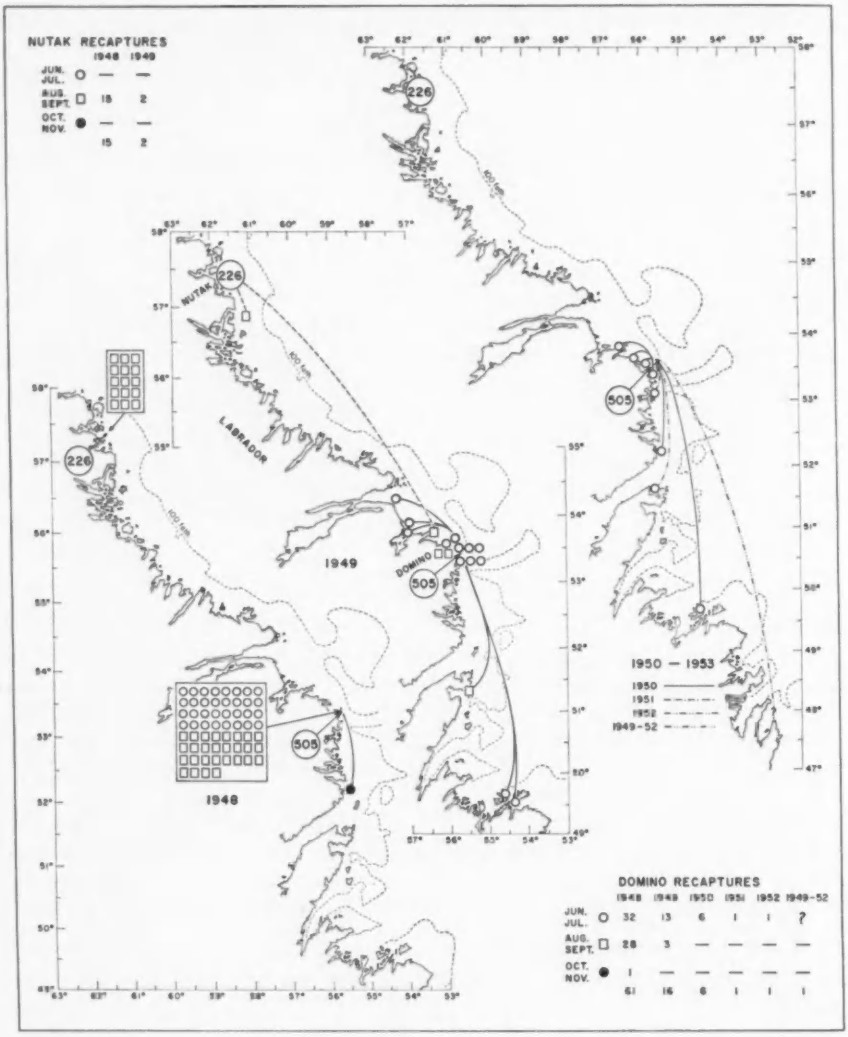

FIG. 8. Recaptures of cod tagged off Nutak, Aug. 12–14, 1948 and off Domino, July 12–22, 1948. (The recapture date of the Domino tag assigned to 1949–1952 was at some time within this period of years and the monthly period of capture was very likely June–July but the exact year is unknown.)

the water above 100–120 fathoms (180–220 m) at this time has a temperature below 0°C, the deeper water is of a higher temperature, but with a maximum even at the greatest depths usually less than 4°C. The area is covered with ice at this season, but as far as we can judge, by relating cod abundance and bottom temperature in similarly deep water elsewhere, the cod are mainly in water

from −0.5 to 2.5°C. Most of these cod spawn before appearing on the coast in June. In this deep, warm water there is no barrier to migration along the coast, and very likely many migrations are carried out in these depths between winter and early summer.

Thus, from the Domino tagging in 1948, although the single fish caught outside the tagging area in the tagging year had travelled southward only to the northern border of the Strait of Belle Isle, 2 of these tagged fish were caught at the beginning of fishing in June and July 1949, much farther southward at the eastern entrance to Notre Dame Bay. These fish had probably travelled a good part of this distance over winter and spring in the deep water.

Thompson's (1943, charts IVa, IVb and V) account of the recaptures of cod tagged in southern Labrador at Camp Islands, Indian Islands, Grady, Shoal Bay and White Islands during 1933–1935 shows migration paths similar to those of our tagging at Domino (Fig. 8). Recaptures from Thompson's tagging showed that there was some movement northward and some slightly into the Strait of Belle Isle, but most of the recaptures were on the Labrador coast and on the northeast coast of Newfoundland; only one fish passed along the east coast beyond the Notre Dame Bay region to the Avalon Peninsula shore south of St. John's.

Englee

Five hundred and seventy-nine cod were tagged at Englee during Sept. 8–19, 1947 (Fig. 9). Since the tagging was late in the fishing season only limited movements were shown during the year of tagging.

In the following year most of the recaptures were distributed away from the tagging location, over an area extending northward 110 nautical miles (200 km) to the Strait of Belle Isle and southward 160 nautical miles (300 km) to Bonavista. Only the southerly part of this migratory pattern was evident in succeeding years. The entire migration was confined to the northeast coast of Newfoundland and the Strait of Belle Isle.

Although there was little southward movement evident from the tagging area during the tagging year the 4 recaptures on the western side of Notre Dame Bay on June 7, 14 and 19, 1948, were all from linetrawl in deep water of 150, 160 and 200 fathoms (270, 290 and 370 m) which is generally less than 1 or 2 miles (1½–3 km) from shore in this area. It is evident that these had migrated over winter and spring in the deep, warm water below the cold layer. The 2 recaptures in Bonavista Bay were in July following the tagging year. It is very likely that these fish also accomplished their main migrations over winter and spring in the deep water. Similarly, in August and September, 1949, both recaptures in Bonavista Bay were in deep water, 140 fathoms (260 m) in one case and reported captured from deep water in the other. These 2 fish, also, very likely migrated in the deep water.

St. John's

The tagging of 577 cod in the St. John's area took place from Oct. 5 to Nov. 4, 1948 (Fig. 10).

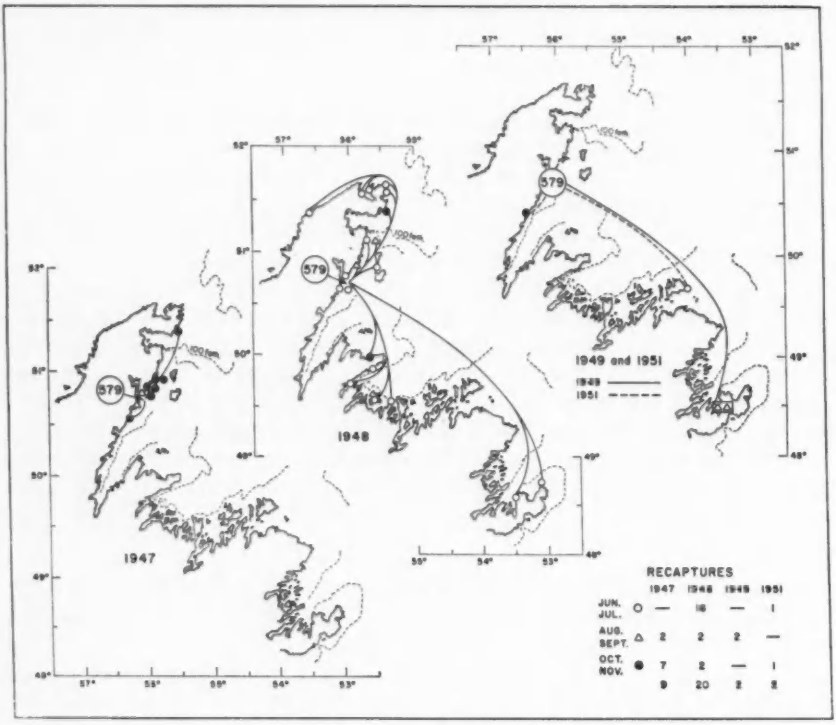

FIG. 9. Recaptures of cod tagged off Englee, Sept. 8–19, 1947.

Tagging was late in the fishing season and recaptures during the tagging year were in the neighbourhood of the tagging area. In the following 3 years, 1949–1951, there were restricted coastwise movements northward as far as Cape Freels and southward and westward to Placentia Bay, but most of the recaptures were not more than 60 nautical miles (110 km) north or south of the tagging area. There were more northward than southward recaptures and few St. John's cod were recaptured west of Cape Race. There was limited movement to the deep, warm water below 100 fathoms (180 m) north of the Grand Bank and southward to the Halibut Channel. A recapture on the northwestern edge of the Grand Bank in April, another recapture on the northern tip of the Grand Bank on June 8 and a recapture in the southern part of the Halibut Channel in March indicate some over-wintering in these areas.

By 1952–1955 several of the recaptured fish had moved northward about 300 nautical miles (560 km) to the northern tip of the east coast of Newfoundland. There was still no significant westward movement along the south coast of Newfoundland.

Thompson's cod tagging at Bay Bulls, about 16 nautical miles (30 km) south of St. John's, between 1933 and 1937 showed no movement to the Grand Bank and a southward record in the Haddock Channel. The inshore recaptures showed exactly the same extent and kind of movement indicated in our tagging, northward along the east coast as far as Pistolet Bay and lesser numbers westward as far as Trepassey Bay (Thompson, 1943, chart I).

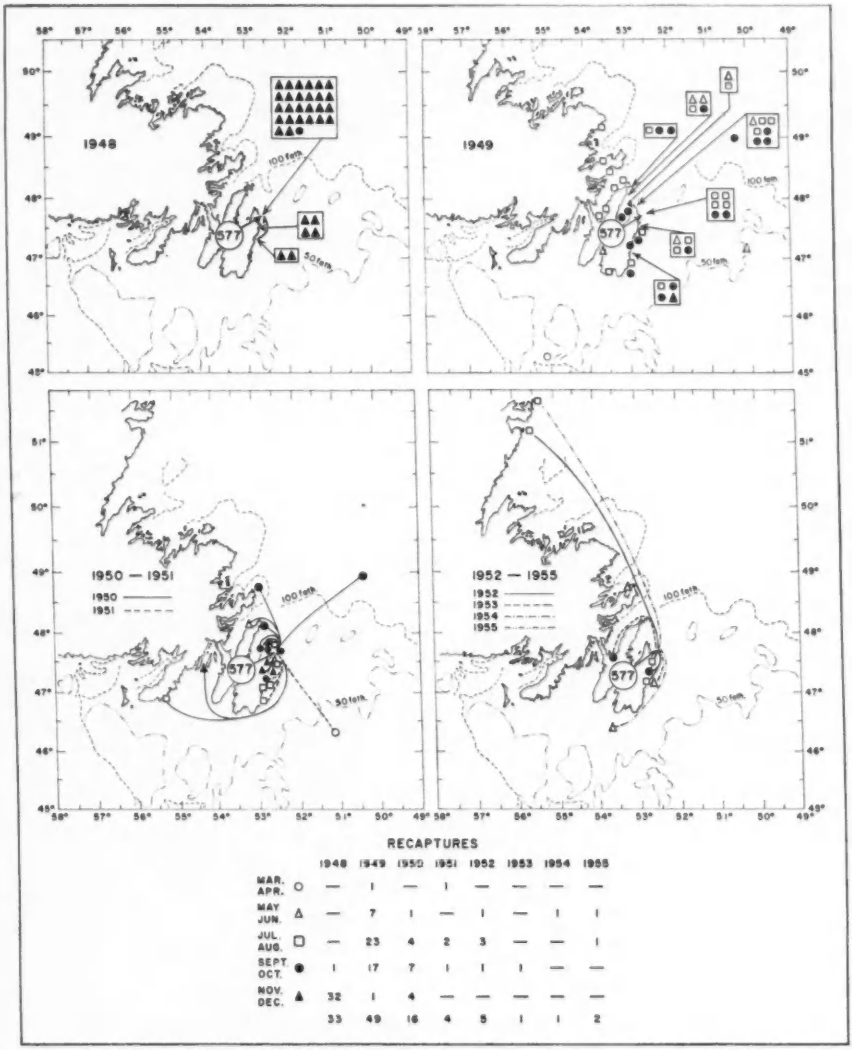

FIG. 10. Recaptures of cod tagged off St. John's, Oct. 5 to Nov. 4, 1948.

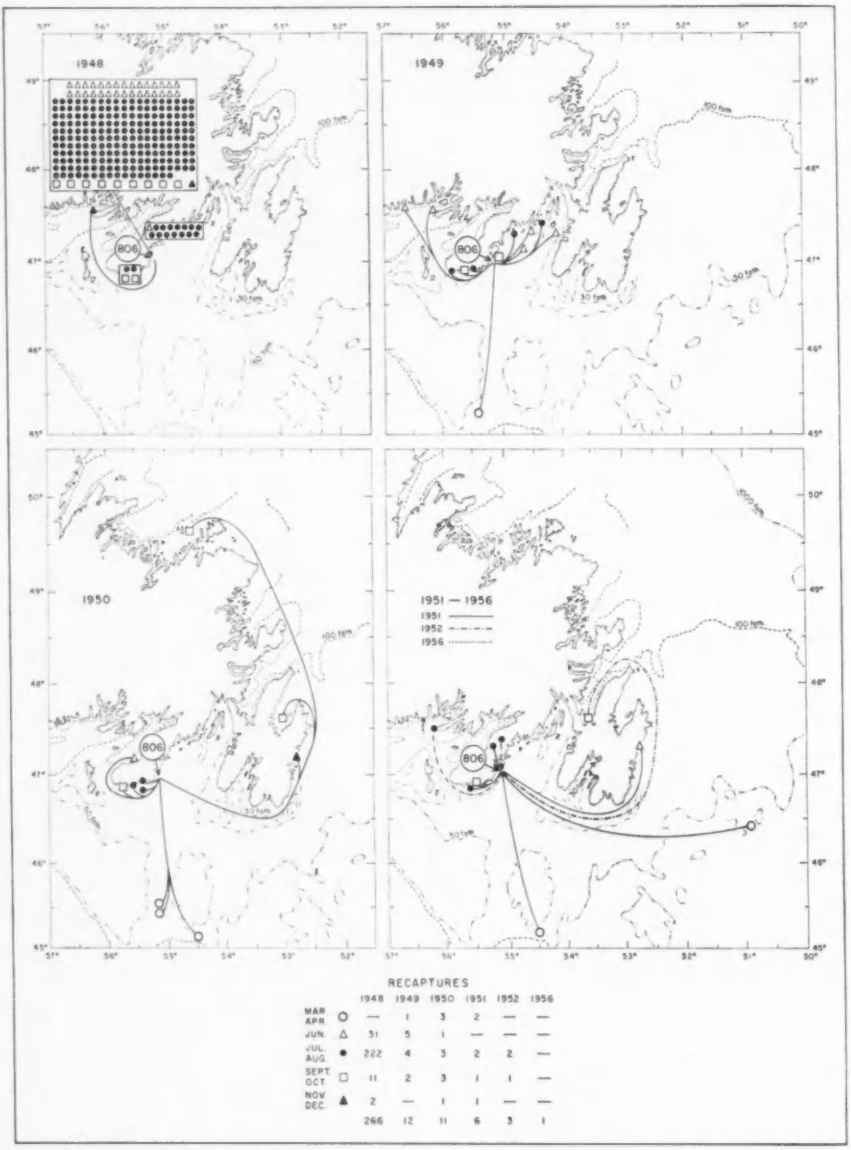

FIG. 11. Recaptures of cod tagged off Burin and Corbin, June 19 to July 10, 1948.

Burin and Corbin

Eight hundred and six cod were tagged at Burin and Corbin between June 19 and July 10, 1948 (Fig. 11). Very little movement was indicated during the remainder of the fishing season of the tagging year. In the year following tagging there was limited distribution east and west of the tagging point and in succeeding years occasional fish were recaptured on the east coast of Newfoundland and one on the Grand Bank.

There is a good indication of a winter movement offshore from the Burin-Corbin area through the Halibut Channel between St. Pierre and Green Banks and possibly through the Haddock Channel between Green Bank and the Grand Bank. There were 5 recaptures, 2 in March and 3 in April, from the central or southern parts of these channels.

Lark Harbour

During Oct. 7–20, 1948, 461 cod were tagged off Lark Harbour (Fig. 12 and 13). All except one of the recaptures, during the remainder of the tagging year, were from the general neighbourhood of the tagging area. In the years following there were many recaptures outside the Gulf in the Rose Blanche

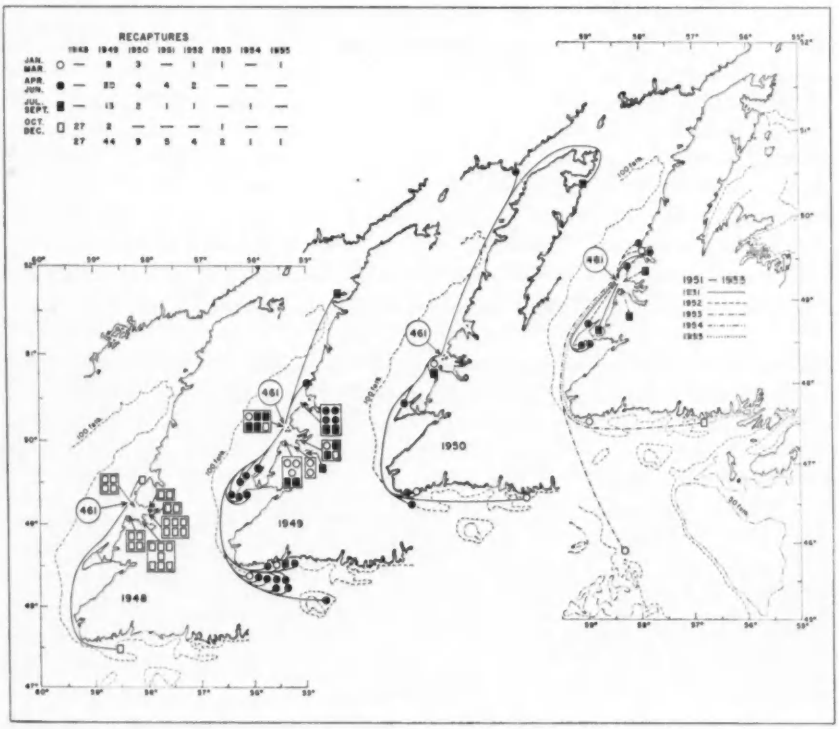

Fig. 12. Recaptures, in different years, of cod tagged off Lark Harbour, Oct. 7–20, 1948.

FIG. 13. Recaptures, in different months, of cod tagged off Lark Harbour, Oct. 7–20, 1948.

Bank and neighbouring coastal areas during the winter and early spring with occasional somewhat more distant recaptures on Burgeo Bank and in the coastal waters as far east as Cape La Hune. There were no recaptures as far east as St. Pierre Bank, although there was one recapture on the northwestern part of the Nova Scotian Shelf.

There was a strong indication that the final completion of the southward migration out of the Gulf of St. Lawrence was in late winter or early spring since the 20 southward recaptures outside the Gulf were caught as follows: December, 2; February, 3; March, 3; April, 10; May, 1; July, 1; (Fig. 13). The recaptures off the Port au Port Peninsula: April, 3; May, 5; June, 2; July, 1; indicate that many of these cod were caught during the return migration into the Gulf from the south coast of Newfoundland.

Thompson (1943, chart II) shows the distant recaptures from tagging near Long Point, Port au Port, about 30 nautical miles (56 km) south of Lark Harbour,

in July and September 1934 and 1935. The pattern of distant migrations was similar to that found in our tagging. One fish passed through the Strait of Belle Isle to Fogo. Most recaptures were obtained from the southwest coast of Newfoundland, the farthest recaptures to the east being seaward on Burgeo Bank and coastward to near the western side of Hermitage Bay.

In our 1948 tagging (Fig. 12) there was much more indication of a southward than of a northward movement from Lark Harbour. Three recaptures only were at significant distances to the northward, one of these moving to the southern end of the Strait of Belle Isle and one through the Strait to Hare Bay. The channel through the Strait of Belle Isle at its shallowest cross-section is only about 35 fathoms (65 m) deep whereas the depth of Cabot Strait is over 200 fathoms (370 m). Most cod are to be found deeper than 35 fathoms (65 m) by late autumn and during the winter the Strait of Belle Isle is filled to the bottom with water below -1°C, but temperatures of $+1$ to $+3$°C, suitable for cod, are present throughout the year in the deep water of Cabot Strait. There is, therefore, a much shorter period of migration outward through the Strait of Belle Isle compared with Cabot Strait where migration can occur at any month of the year.

Grand Bank and St. Pierre Bank, 1947

The Grand Bank and St. Pierre Bank tagging from which recaptures were obtained was carried out from May 2 to June 8 (Fig. 14). All tagging was on the southern parts of these banks and from both banks there was some migration toward the eastern part of the south coast of Newfoundland. The other migrations on the Grand Bank were late spring and summer movements over the central part of the bank. One of the tagged cod was recaptured on Sable Island Bank, 10 years after being tagged. From St. Pierre Bank there is evidently an overwinter movement into the southern part of the Halibut Channel and in the late winter-early spring there are usually concentrations of cod in this area.

In the year of tagging 2 cod were recaptured in July, after spawning, on the eastern part of the south coast of Newfoundland. There were 2 similar migrations in June and July of the following year. These movements were over the Avalon Channel and the western extension of this channel north of St. Pierre Bank. In this channel, at the time these movements were carried out in summer, the temperature of the bottom water is usually below -1°C. It is evident from our longlining and otter-trawling experiments that these temperatures below -1°C are usually unsuitable for cod of commercial size. In the late spring cod are present in the surface layers near the Newfoundland east coast where they sometimes caught on floating longlines. When cod first appear on the east coast they often follow the pelagic capelin into water 1 or 2 fathoms (2–4 m) deep and during the month of June may be found mainly in 5–10 fathoms (10–20 m), with extreme scarcity in deeper water approaching -1.0°C in temperature. It is evident, therefore, that these long and rapid migrations over the low-temperature deeper water are made in the warmer upper layers, rather than along the bottom. (For a more complete discussion of these matters and of the hydrography of the Avalon Channel see Templeman and Fleming, 1956.)

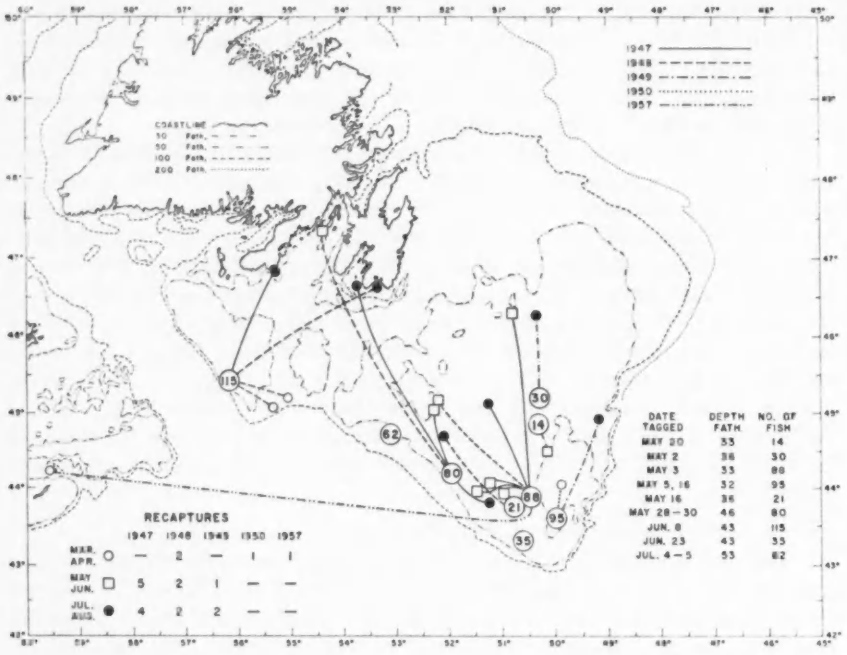

FIG. 14. Recaptures of cod tagged on the Grand Bank and St. Pierre Bank, May 2 to July 5, 1947.

It is very likely, also, from these recaptures, that some of the cod which spend the summer on the eastern part of the south coast of Newfoundland spend the winter on the southern parts of St. Pierre Bank and of the Grand Bank and probably spawn there or on the journey through the surface layers to the coast.

There is some late spring and summer migration northward on the Grand Bank and their vertebral numbers indicate that the cod of the southern and of the central portions of the Grand Bank are parts of the same stock. The St. Pierre Bank tagging was probably too late (June 8) to obtain the complete picture of onshore migration in the tagging year.

GRAND BANK AND ST. PIERRE BANK, 1948

Tagging took place between April 23 and June 8 but the only tagging resulting in tag returns was on the northwestern part of the Grand Bank on June 4–5, on the northern part of the central Grand Bank on June 6 and on the northwestern edge of St. Pierre Bank on April 23 (Fig. 15).

Cod caught by the otter trawl of the *Investigator II* mainly in 37–51 fathoms (68–93 m) on the northwestern edge of the Grand Bank and tagged on June 4–5 were spawning or spent and were feeding heavily on capelin. Several weeks later, when the capelin came inshore to spawn, 4 of these tagged fish were re-

captured inshore on the western side of the Avalon Peninsula on June 26, 30 and July 4, 12. (Capelin begin to spawn on the east coast of Newfoundland in the latter part of June and continue to spawn on the beaches during early July (Templeman, 1948).) These cod approached shore so quickly that they probably followed the pelagic capelin from the Grand Bank to the shore of the Avalon

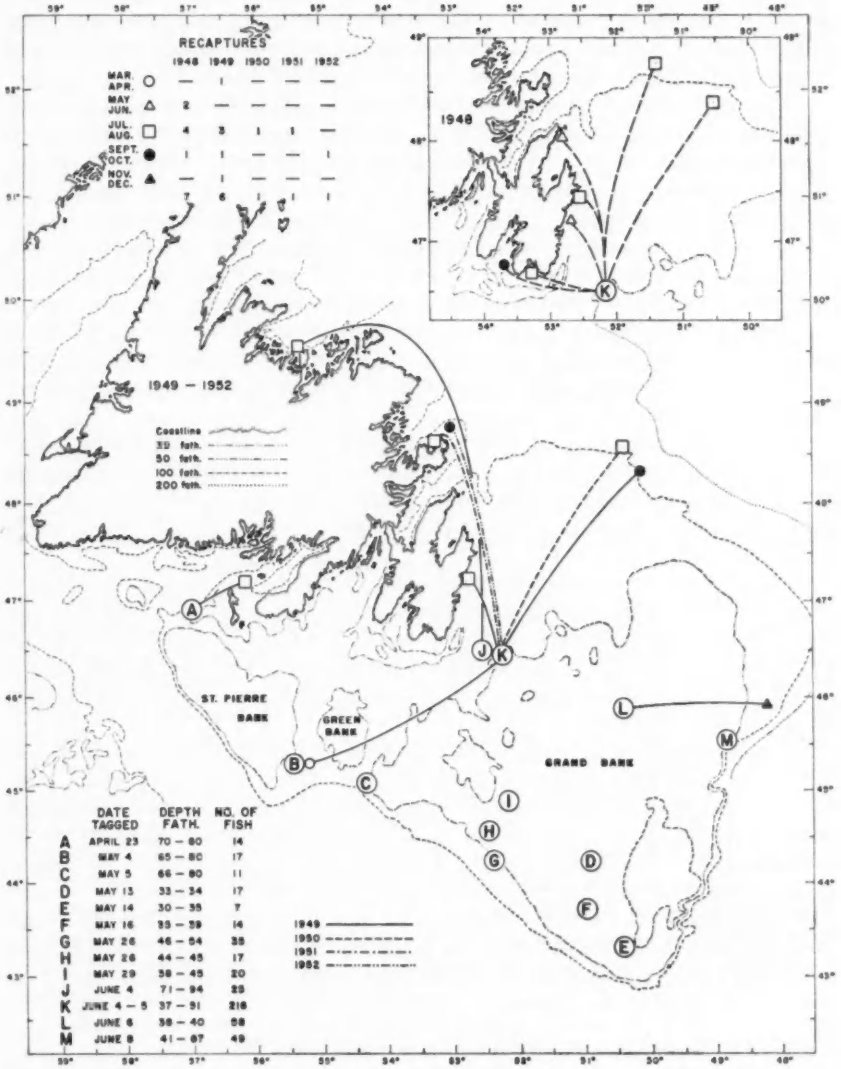

FIG. 15. Recaptures of cod tagged on the Grand Bank and St. Pierre Bank, April 23 to June 8, 1948.

Peninsula. Another of these cod was caught on the western side of the Avalon Peninsula in October and 4 more were caught inshore in subsequent years but by this time they had distributed themselves between the Avalon Peninsula and Notre Dame Bay. As we have said for the short-term recaptures in Newfoundland from the Grand Bank and St. Pierre Bank tagging in 1947, there is every evidence that the fish recaptured in the year of tagging, and probably also those of subsequent years, travelled in the upper water layers over the deep water of the Avalon Channel between the Grand Bank and the coast and not along the bottom (Templeman, MS, 1951 and Templeman and Fleming, 1956).

The appearance of abundant cod on the east coast of Newfoundland generally coincides with the time of spawning of very great quantities of capelin on and near the beaches. The capelin form almost the sole food of these cod at this time. The results of the tagging discussed above give some evidence that the cod, pelagic after spawning, follow the pelagic capelin to the beaches.

It is also very likely from the recaptures that many cod of the eastern section of the Avalon Peninsula over-winter and spawn on the neighbouring northwestern portion of the Grand Bank, returning to the coast with the advancing capelin shoals mainly in June. There is a strong indication also that some of the cod over-wintering and spawning on the western edge of the Grand Bank later migrate into water mainly deeper than 100 fathoms (180 m) on the northern slope of the Grand Bank.

There was only one recapture to the southward of the tagging area. This was a March recapture in the Halibut Channel in the year following tagging and very likely indicates a wintering area since a number of cod tagged in more recent years near the Avalon Peninsula have been caught during the early spring in this Channel.

There were no inshore recaptures from 58 cod tagged on the central part of the Grand Bank in 38–40 fathoms (70–73 m) on June 6 and no recaptures from 49 cod tagged on the eastern portion of the Grand Bank in 41–67 fathoms (75–123 m) on June 8. Also there were no reported recaptures from 138 cod tagged on the southern and western parts of the Grand Bank and in the channels near Green Bank in May 1948.

The previous cod tagging on the southern part of the Grand Bank in late June 1934, and more extensively in July 1935, (Thompson, 1943, chart VII) gave results essentially similar to our own. Most of the on-the-bank migrations were toward the central part of the bank and there was some migration to the southern parts of the Avalon and Burin Peninsulas. In addition one fish moved to St. Pierre Bank and one to the deep water to the north of the bank.

Thompson's St. Pierre Bank tagging in July 1935 was more extensive than ours and showed recaptures along the whole width of the south coast of Newfoundland as well as some on St. Pierre Bank itself, the Grand Bank and 2 on the Nova Scotian banks (Thompson, 1943, chart VI).

Depths of Recapture of Tagged Cod in Different Months

Cod brought to the surface for tagging often have broken swim bladders and consequently, for some time after tagging their depth relationships may not be

quite normal. Also, most cod caught and liberated in the middle of a concentration of fishing effort may be recaptured before they can redistribute themselves. This was the case for the Burin-Corbin cod caught by trap and tagged in June and July and mostly caught in the same area within a month after tagging. Thus, we have thought it wise to eliminate from the tables of depths of recapture cod recaptured during the tagging year. Also, information on depth of recapture was not available for all recaptures. In the following discussion all references to depths of recapture will refer to recaptures excluding the year of tagging.

All recaptures from the Domino-Nutak tagging (Table I and Fig. 8) were in shallow water of 5–20 fathoms (9–37 m) in July and August but almost entirely in July, the month when large quantities of cod are caught in these areas by trap in shallow water. There were no deep-water recaptures. At the time these recaptures were being made there was no offshore or deep-water fishery in the Labrador area, the European trawler fishery in this area beginning in 1952 and becoming large only in 1953.

The few recaptures from the Englee tagging (Table I, Fig. 9) were mainly from shallow water, 11–20 fathoms (20–37 m), in June-July; down to 51–60 fathoms (75–110 m) by October; and partly from deep water, 131–200 fathoms (240–366 m), chiefly in June before the inshore migration had begun, but with one deep-water August recovery. These depth distributions, although from only a few cod, illustrate the custom of the cod of the northeast coast of Newfoundland to spend the winter in the deep water more or less adjacent to the coastal waters. Most of the smaller fish return in June and July to the shallower coastal areas, but great numbers of the larger fish remain throughout the summer in the deep water offshore (Templeman and Fleming, 1956).

Recaptures from the St. John's tagging (Table I, Fig. 10) showed almost all the recaptures to be in the shallow-water inshore area in 11–50 fathoms (20–91 m) with an occasional early spring recapture in the deeper water to the south and occasional summer recaptures in the deep water to the north. The inshore recaptures were almost all taken in very shallow water, 11–20 fathoms (20–37 m), by trap in June and July; an equally large number of cod were in 21–30 fathoms (38–55 m) and some in 31–40 fathoms (57–73 m) by August. From July-November the shallow-water fish were recaptured progressively at slightly greater depths as the layer of water with temperature below 0°C retreated further below the surface. For a more detailed discussion of the seasonal hydrographic changes in the St. John's area see Templeman and Fleming (1956).

Recaptures from the Burin-Corbin tagging (Table I, Fig. 11) were mainly in the deeper water to the southward in March–April and in the shallow water 11–20 fathoms (20–37 m) in June–August. Several deep-water recaptures in summer were close to the coast.

Recaptures from the Lark Harbour tagging (Table II, Fig. 12, 13) were from 11–20 fathoms (20–37 m) in June, gradually occurring more deeply (21–50 fath, 38–91 m) by September when the surface layers were warmer and the intermediate cold water layer further below the surface, and progressively more

deeply as the surface layers chilled, to 61–130 fathoms (112–238 m) in February–March. In April the fish were shallower and by May, although some individuals remained fairly deep, others were in water as shallow as 5–10 fathoms (9–18 m) pursuing the herring which spawn at this time in shallow water.

Although returns from the Grand Bank and St. Pierre Bank tagging were few, recaptures showed several somewhat different tendencies depending on the stock relationships of the cod (Table II, Fig. 14, 15). The few recaptures from the St. Pierre Bank tagging were mainly from the deep water of the Halibut Channel in spring and from the inshore shallow water in summer. These depth relationships and localities of recaptures in different seasons were similar to those

TABLE I. Depths of recapture (excluding tagging year) for cod tagged in the inshore areas off Domino-Nutak, Englee, St. John's and Burin-Corbin in 1947–1948.

Depth range		Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Total
fath	*m*										
DOMINO-NUTAK											
5–10	(9–18)	..	..	..	..	1	..	..	..	..	1
11–20	(20–37)	..	..	..	..	15	2	..	..	..	17
ENGLEE											
11–20	(20–37)	..	..	..	3	4	..	..	..	..	7
21–30	(38–55)	..	..	..	..	..	2	..	..	..	2
31–40	(57–73)	..	..	..	..	1	..	..	..	..	1
41–50	(75–91)	..	..	..	..	..	..	..	1	..	1
51–60	(93–110)	..	..	..	..	..	..	..	1	..	1
131–140	(240–256)	..	..	..	..	..	1	..	..	..	1
141–150	(258–274)	..	..	..	2	..	..	..	..	..	2
151–160	(276–293)	..	..	..	1	..	..	..	..	..	1
191–200	(349–366)	..	..	..	1	..	..	..	..	..	1
ST. JOHN'S											
11–20	(20–37)	..	..	..	7	14	6	2	..	..	29
21–30	(38–55)	..	..	1	..	..	6	10	1	1	19
31–40	(57–73)	..	..	..	..	2	2	5	3	2	14
41–50	(75–91)	..	..	..	1	..	..	..	1	1	3
81–90	(148–165)	1	..	..	..	..	..	..	..	..	1
131–140	(240–256)	..	..	..	..	..	..	1	..	..	1
151–160	(276–293)	..	..	..	..	..	..	1	..	..	1
BURIN-CORBIN											
11–20	(20–37)	..	..	..	4	7	2	..	..	..	13
21–30	(38–55)	..	..	..	..	..	..	1	1	..	2
31–40	(57–73)	1	..	..	..	1	..	..	..	..	2
51–60	(93–110)	1	..	..	1	..	..	..	..	..	2
71–80	(130–146)	..	1	..	..	..	..	..	..	..	1
81–90	(148–165)	1	2	..	1	..	..	..	..	..	4
91–100	(166–183)	..	..	..	..	1	..	..	..	..	1

TABLE II. Depths of recapture (excluding tagging year) for cod tagged (1) off Lark Harbour; (2) on the Grand Bank and St. Pierre Bank; and

TABLE II. Depths of recapture (excluding tagging year) for cod tagged (1) off Lark Harbour; (2) on the Grand Bank and St. Pierre Bank; and (3) the total for all inshore areas, including Nutak and Lark Harbour, but excluding the Grand and St. Pierre Banks, 1947–1948. (March is repeated so that the trend can better be followed, but it is not duplicated in the totals.)

Depth range		Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Total
fath	*m*														
LARK HARBOUR															
5–10	(9–18)	..	..	1	..	..	..	..	..	..	..	..	..	..	1
11–20	(20–37)	..	..	1	3	1	..	..	..	..	..	..	..	..	5
21–30	(38–55)	..	1	..	..	..	3	2	..	1	..	..	..	..	7
31–40	(57–73)	..	1	..	..	1	..	1	..	..	..	..	..	..	3
41–50	(75–91)	..	..	1	..	..	..	1	..	..	..	1	..	..	3
51–60	(93–110)	..	1	..	..	..	..	..	..	..	1	1	..	..	3
61–70	(112–128)	..	3	..	..	..	..	..	..	..	1	..	1	..	5
81–90	(148–165)	2	6	1	..	..	..	..	..	..	..	..	1	2	10
121–130	(221–238)	1	..	..	..	..	..	..	..	..	..	..	..	1	1
(a) ST. PIERRE BANK; (b) NORTHWESTERN GRAND BANK; (c) SOUTHERN AND CENTRAL GRAND BANK (each letter below represents 1 specimen)															
11–20	(20–37)	..	..	..	..	a	..	..	..	..	..	..	..	..	1
21–30	(38–55)	c	c	..	c	..	b	..	..	..	..	..	..	c	4
31–40	(57–73)	..	..	c	..	..	..	..	..	..	..	..	..	..	1
41–50	(75–91)	..	..	..	..	c	..	b	..	..	..	..	..	..	2
61–70	(112–128)	b	..	..	..	a	..	..	..	c	..	..	..	b	3
81–90	(148–165)	a, a	..	..	..	c	..	..	..	..	..	..	..	a, a	3
91–100	(166–183)	..	..	..	..	b	..	..	..	..	..	..	..	..	1
101–110	(185–201)	..	..	..	..	..	..	..	b	..	..	..	..	..	1
TOTAL: DOMINO-NUTAK, ENGLEE, ST. JOHN'S, BURIN-CORBIN, LARK HARBOUR															
5–10	(9–18)	..	..	1	..	1	..	..	..	..	..	..	..	..	2
11–20	(20–37)	..	..	1	17	41	10	2	..	..	..	..	..	..	71
21–30	(38–55)	..	1	1	..	..	11	13	2	2	..	..	..	..	30
31–40	(57–73)	1	1	..	..	5	2	6	3	2	..	..	..	1	20
41–50	(75–91)	..	..	1	1	..	..	1	2	1	..	1	..	..	7
51–60	(93–110)	1	1	..	1	..	..	..	1	..	1	1	..	1	6
61–70	(112–128)	..	3	..	..	..	..	..	..	..	1	..	1	..	5
71–80	(130–146)	..	1	..	..	..	..	..	..	..	..	..	..	..	1
81–90	(148–165)	4	8	1	1	..	..	..	..	..	..	..	1	4	15
91–100	(166–183)	..	..	..	..	1	..	..	..	..	..	..	..	..	1
121–130	(221–238)	1	..	..	..	..	..	..	..	..	..	..	..	1	1
131–140	(240–256)	..	..	..	..	..	1	1	..	..	..	..	..	..	2
141–150	(258–274)	..	..	..	2	..	..	..	..	..	..	..	..	..	2
151–160	(276–293)	..	..	..	1	..	..	1	..	..	..	..	..	..	2
191–200	(349–366)	..	..	..	1	..	..	..	..	..	..	..	..	..	1

from the Burin-Corbin tagging (Table I, Fig. 11) and show inter-relationships between the cod of these two areas. Recaptures from the tagging on the northwestern Grand Bank showed occasional southward deep-water recaptures in spring, more northwestward deep-water recaptures in summer and autumn and still more inshore shallow-water recaptures in summer. These depth and locality relationships were similar to those from the St. John's tagging (Table I and Fig. 10) but showed a greater proportion with a northwestward deep-water summer distribution. Recaptures during spring and summer from the tagging on the southern and central Grand Bank were from inshore and top of the bank areas of shallow to moderately shallow water, with 2 recaptures in July and November in water of intermediate depths on the eastern slope of the bank.

The over-all depth relationships of recaptures from tagging in all inshore areas (Table II) showed a concentration in water of 11–20 fathoms (20–37 m) in June and July, in 11–30 fathoms (20–55 m) in August, and in 21–40 fathoms (38–73 m) in September. Recaptures were gradually deeper from September to February-March with some movement toward the surface by May. During the summer and autumn there were some recaptures from deep water below 130 fathoms (228 m). Undoubtedly cod are also present in these depths off the northeast coast of Newfoundland and off Labrador during winter and spring but due to the lack of winter otter-trawl fishing in these northern depths during the years when these tags were being returned there were no recaptures from this northern area in the December to May period.

Discussion and Conclusions

Arcto-Norwegian cod stock. Trout (1957) for the Arcto-Norwegian cod stock found cod occupying progressively deeper water with the approach of winter but gradually increasing pelagic behaviour with increasing light in the spring and early summer. He concluded that the winter movement toward the spawning grounds at Lofoten and on the Norwegian coastal areas was a contranatant migration on the bottom in the absence of light during the time of the yearly maximum of water transport. The migration away from the spawning grounds in spring and summer is passive drift in the direction of the current during the lower summer peak of water transport at a time when the cod schools are to a great degree pelagic.

Newfoundland area, general. We are handicapped by lack of knowledge of precise current movements in winter, especially in the deeper water, and of precise spawning dates and areas in the northern parts of the Newfoundland area. However, we shall consider how well the movements of our tagged cod fit into the pattern described by Trout.

In the Newfoundland area the pelagic phase, especially of the smaller mature and at least the larger immature cod, occurs in late spring and early summer. Throughout the summer as the surface waters warm too greatly, and additionally with the advance toward winter and early spring as the upper water layers chill in many areas below the usual temperature tolerance of the cod, their movements are progressively deeper and more bottom related. In the northern areas, where

there is a cold intermediate water layer during the summer time, many of the cod do not take part in the pelagic movement toward the surface but remain all summer below the cold water layer. For a more complete discussion and the evidence for this vertical migration of the younger cod and the relative lack of it in the older cod of the Bonavista area see Templeman and Fleming (1956). The vertical movements and the pelagic phase are essentially the same in the Newfoundland area as in the Bear Island-Barents Sea area. However, the late-spring, early-summer pelagic movements on the northeastern colder part of the Newfoundland coastal shelf do not appear to be diurnally to bottom but usually within the water layer above the thermocline between the upper warmer and the intermediate colder layer. Presumably, also, in the Newfoundland area these movements occur closer to the surface, probably as a rule in 5–15 fathoms (10–30 m), often at night and even during the daytime in pursuit of capelin to the surface. Also, in the northeastern part of the Newfoundland area many cod, especially of the larger sizes, do not take part in this upper layer pelagic movement.

LABRADOR COD. In the Labrador tagging (Fig. 8) the long migrations of cod tagged at Domino in 1948 and recaptured southward in June–July 1949 on the eastern side of Notre Dame Bay have evidently occurred over winter in the deep water near the coastal shelf. These fish apparently moved southward in winter, spring and early summer with the prevailing current.

ENGLEE TAGGING. Similarly in the Englee tagging, September 1947 (Fig. 9) there are southward movements over winter to early summer, apparently with the Labrador Current in the deep water off the coastal shelf, as shown by the southward recaptures in June–July 1948. The early-summer, after-spawning, inward movement around the most northern part of the Great Northern Peninsula of Newfoundland and inward to the Strait of Belle Isle, evident in 1948 from the recaptures from the Englee tagging of 1947 (Fig. 9) and in Jeffers (1931), is northward against the prevailing current which flows outward on the southern side of the Strait of Belle Isle (Huntsman *et al.*, 1954).

GULF OF ST. LAWRENCE AND CABOT STRAIT. In the area of cod movements from the Lark Harbour tagging (Fig. 12, 13) it is well known (Dawson, 1913; Sandström, 1919; MacGregor, 1956) that a current passes inward through Cabot Strait on its northern side and northward along the west coast of Newfoundland. Most of the Newfoundland winter codfishing on the western part of the south coast of Newfoundland is at 60–90 fathoms (110–165 m) and the European trawler fishery near the southwest coast of Newfoundland is (according to McCracken and Clark, MS, 1958) at about 45–165 fathoms (80–300 m) but mainly about 110 fathoms (200 m). It is therefore apparent that the over-winter migration outward is southward against the prevailing current as in Trout's Arcto-Norwegian cod stock.

Some of the movement inward in late spring and early summer may be in the deep water where the inward current is weak, but very likely much of it, as occurs with cod generally around the Newfoundland coast, is in the upper

layers. Thus, there is a regular May "herring-run" of cod to St. George's Bay which was observed by the senior author in May 1945. These fish run into shallow water of 6 fathoms (11 m) or less, a good indication that they are migrating in the surface layer.

On the southern or Cape Breton side of Cabot Strait a similar southward (southeast) winter movement of cod tagged off Northern New Brunswick occurs in June-September outward from the Gulf of St. Lawrence and a late spring and summer movement northward (northwest) into the Gulf (McCracken, 1959; McKenzie, 1956). These cod in winter and spring are caught mainly in the vicinity of 110 fathoms (200 m), off the east coast of Cape Breton Island, chiefly outside the Gulf of St. Lawrence but with some as far westward in the Gulf as the Bird Rocks area near the Magdalen Islands. In summer and autumn they are caught almost entirely off northern New Brunswick and the neighbouring Gaspé coast mainly at a depth less than 50 fathoms (90 m). The recapture of so few cod on the Newfoundland side from the New Brunswick tagging and on the Nova Scotian side from the Newfoundland tagging indicates that the outward movement is in relation to the bottom and that the main body of cod does not go deeply enough to cross the bottom of the Laurentian Channel which is over 200 fathoms (370 m) deep and that only a small proportion of these two stocks crosses this channel either pelagically or on the bottom. It would be expected, in any case, that the cod would return in summer toward the general area where they were tagged. Apparently, the outward movement from the southern side of the Gulf is mainly in water between 50 and 110 fathoms (90–200 m) deep with a probable tendency toward the greater rather than the lesser of these depths. The inward movement in late spring and summer at first may be mainly in 60–110 fathoms (110–200 m) and later undoubtedly shallower, as on the Newfoundland side, since the fish during the summer are mainly caught in depths less than 50 fathoms (90 m).

In these depths the shallower-water cod are proceeding southwards out of the Gulf in the winter with the Gaspé-Cape Breton Currents and northward into the Gulf in late spring and summer against these currents. For the deeper-water cod, near the 200-metre level, on the Cape Breton side it appears to be doubtful from MacGregor (1956) whether there is a weak inward or a weak outward current.

Information is limited with regard to the spawning condition of these migratory fish. McCracken and Clark (MS, 1958) recorded the sexual maturity stages of otter-trawled cod caught by French trawlers during late March 1958, mainly in about 110 fathoms (200 m) in ICNAF Division 4R off the west coast of Newfoundland. From Cape Ray to Cape St. George in 98 mature female cod 83% were ripening, 14% ripe and 3% spent-recovering, whereas north of Cape St. George, off Bay of Islands, in 26 mature female cod 58% were ripening, 8% ripe, 20% spawning and 14% spent-recovering. In ICNAF Division 4T, northwest of Bird Rocks, of 12 mature female cod 50% were ripening and 50% spent-recovering and in Division 4V, off St. Paul's Island, of 21 mature female cod, 85% were ripening, 10% ripe and 5% spent-recovering.

Observations on sexual maturity were made by experienced technicians of the St. John's Station at Isle aux Morts during winter and spring in 1952 and 1957 on cod caught in 60–90 fathoms (110–165 m) which, from our tagging returns, should be approximately of the same stock as that examined by McCracken and Clark in the southern part of ICNAF Division 4R. The results, for mature females only, were classified into 5 groups:

A: Spawned previous year, and new eggs not visible
B: All eggs opaque; will spawn in present year
C: Some clear eggs present, but less than 50% of bulk of eggs clear
D: 50% or more of bulk of eggs clear
E: Spent and with new eggs not visible

The percentages of these types among mature female cod were as follows:

Year	Date	No.	A	B	C	D	E
			%	%	%	%	%
1952	Feb. 21–Mar. 4	161	14	86	0.6	0	0
1957	Mar. 7–13	104	0	99	1	0	0
1957	Apr. 16–18	114	..	82	11	4	4

During the period Feb. 21 to Mar. 4 only 0.6% of the mature females possessed some clear eggs and none had more than 50% of the bulk of the eggs clear. The general female population was not at all close to the ripe and spawning conditions, yet spent females made up 14% of the samples; these had spawned during the previous year. In the following period Mar. 7–13 only 1% of the population had any clear eggs and none had more than 50% of the bulk of the eggs clear. Apparently, again, spawning had not begun. By Apr. 16–18 there were still only 4% of the female cod with more than 50% of the bulk of the eggs clear. The 4% spent were probably still mainly or entirely fish which had spawned in the previous year. The senior author observed the shallow-water "herring-run" of cod to St. George's Bay, Newfoundland in the last week of May 1955 and noted that in general the cod ovaries were full and spawning had not yet occurred. This, however, was only a casual observation without examination and recording of maturities of individual cod. Mature cod examined by the junior author in Port aux Basques, June 2–9, 1949, were 98% spent. This spawning occurred not later than May and probably began in April. Inshore cod from the same general area, caught and examined at Isle aux Morts on July 4, 1957, were mainly spent fish of that year but there were still some females with large well-developed opaque (but no clear) eggs which probably would not spawn before August. However, it is probable that these cod at Isle aux Morts in July were mainly local southwest coast and Burgeo Bank cod, not the migratory Gulf stock.

The evidence, therefore, regarding spawning is a little conflicting and deserves more detailed study. Part of the difference between McCracken and Clark's results and our own is doubtless due to differences in the terminology used in recording the stages of sexual maturity. Different schools, however, may spawn

at somewhat different times. It is well known that many cod spawning in the Gulf of St. Lawrence do so during the summer and early autumn from June–October (Bigelow and Welsh, 1925; Templeman, MS, 1951; McKenzie, 1956), and this is supported by unpublished data of the Fisheries Research Board Biological Station, St. John's. On the other hand, spring spawning is common on the Newfoundland and Nova Scotian banks.

It is possible that the local cod in the deep-water wintering area spawn earlier than the cod migrating further into the Gulf and that the cod moving into the Gulf on the Newfoundland side may be migrating inward as a preliminary to later spawning in the Gulf.

There is no evidence that cod are forced out of the Gulf by low temperature. Very likely there is earlier chilling of the waters of the same depths to the north on the Newfoundland side and to the west on the Canadian mainland side of the Gulf which may give an outward stimulus. However, below approximately 100 fathoms (180 m) in the Gulf, water from above 0° to over 5°C is present all year round. Thus, cod could spend the winter in the deep channels of the Gulf while the overhead water is reduced to below 0°C or below -1°C. It is very likely that the large bodies of cod moving out of the Gulf in the late fall and early winter and returning in late spring and early summer are responding to hereditary patterns which over the period of development of these cod stocks have been advantageous to them from the point of view of survival, growth and reproduction. The same kind of statement is likely to be true of all major fish migrations operating on a yearly cycle.

Grand Bank and St. Pierre Bank. In the tagging on the southern Grand Bank and southern St. Pierre Bank, May 2 to June 8, 1947, although movement in subsequent years can only be inferred, most of the fish passed northward against the Labrador Current in the early summer of the tagging year, probably after spawning, to be caught further northward on the central area of the Grand Bank or inshore. Studies at the St. John's Station show correspondingly low vertebral numbers for cod of the central and southern Grand Bank. Also, an early March survey has shown that at this season the central part of the Grand Bank is largely depopulated of cod which have apparently moved to the southern slopes of the bank. It is thus indicated that most of the cod from the Grand Bank central area are of the same population as that on the southern slopes of the bank. The commercial concentrations of cod and haddock southward on this bank in winter, with northward shifts of the population in late spring and early summer, are indicative of southward movements in the direction of the Labrador Current in late autumn and winter to wintering and spawning areas, and northward movements after-spawning or coincident with spawning in late spring and early summer against the Labrador Current. In the St. Pierre Bank area in late winter and early spring there have often been great concentrations of cod fished commercially in the southern part of the Halibut Channel between St. Pierre Bank and Green Bank. These concentrations are far greater than are to be expected from the relatively small quantities of cod on St. Pierre Bank in summer. It is indicated by Fig. 11 and 14 that some

of the cod from the eastern part of the south coast of Newfoundland spend the winter and early spring in the Halibut Channel. This involves a winter movement southward, mainly in the direction of the Labrador Current, a branch of which passes through the Halibut Channel, and a northward movement against the current in the spring either immediately after or just before spawning.

The cod tagged on the northwestern slope of the Grand Bank on June 4–5, 1948, were spawning. Immediately after spawning (since the cod appearing on the Newfoundland coast are spent) some of the tagged cod moved inshore northward against the Labrador Current and to a lesser degree westward across this current, coincident with the appearance of capelin on shore. Capelin were very numerous in the localities where the cod were tagged and the cod were feeding heavily on them. Possibly the capelin and some of the cod moved inshore at the same time. There was also some summer movement northward against the Labrador Current to the offshore deeper water at the northern slope of the Grand Bank.

Conclusions. It is thus apparent that in the parts of the Newfoundland area for which it is possible to obtain information on winter occurrences of tagged cod there is no general agreement with Trout's thesis of a southward over-winter movement against the current and a northward after-spawning pelagic surface movement in the direction of and aided in great degree by the current. There is, indeed, presumably a bottom-related progression to deeper water in winter before spawning, sometimes against the current but on the east coast of Newfoundland and on the Newfoundland banks apparently usually with the current. There is an onshore movement in May–June after spawning or coincident with spawning, apparently pelagically in the surface layers, but mainly on the southeast coast of Newfoundland against the current. The one constantly occurring picture is a generally southward winter and a northward spring and early summer movement regardless of the direction of the current. The picture is not clear off northeast Newfoundland and southern Labrador since little information is available due to ice coverage in winter and spring. Here the cod (Templeman and Fleming, 1956) move offshore along the bottom over winter to deep warmer water which is often close by the summer shallow water abode of the cod. The onshore spawning or after-spawning movement of the smaller cod is apparently pelagic and generally coincident with the appearance of the capelin on shore. This movement, if the cod move directly from above the deep water toward shore, is to some extent across and to some extent with the Labrador Current since this current has both a southward and onshore set.

RECAPTURE RATES

Yearly and Total Recaptures

Table III shows the numbers of cod of various size ranges tagged and the percentage authenticated recaptures (returns) of tagged cod during the tagging year and for each of the first 10 years after tagging. The year of tagging is that part of the calendar year remaining after tagging and the other years are calendar years.

TABLE IIIA. Recaptures of cod tagged in the Newfoundland area, 1947 and 1948. Dates, depths and methods of capture for the 7 taggings were as follows:

A—Sept. 8–19, 1947, 40–80 fathoms, trawl
B—May 2 to July 5, 1947, and May 5 to June 8, 1948, 27–94 fathoms, ottertrawl
C—June 8, 1947, and April 23 to May 4, 1948, 30–80 fathoms, otter trawl
D—July 12 to Aug. 20, 1948, 12–15 fathoms, cod trap
E—Oct. 5 to Nov. 4, 1948, 25–75 fathoms, linetrawl and handline
F—June 19 to July 10, 1948, 15–16 fathoms, trap
G—Oct. 7–20, 1948, 17–24 fathoms, handline
(I = internal flat tag; E = bachelor-button opercular tag)

Length (*cm*) when tagged	A Englee E	B The Grand Bank E	C St. Pierre Bank E	D Nutak and Domino I	D Nutak and Domino E	E St. John's I	E St. John's E	F Corbin and Burin I	F Corbin and Burin E	G Lark Harbour I	G Lark Harbour E
	NUMBER OF COD TAGGED										
41–49	...	5	18	...	...	22	31	...	...	8	7
50–60	195	27	39	118	384	113	91	79	272	37	33
61–70	283	157	51	41	169	80	94	115	249	44	53
71–80	76	270	26	6	8	49	40	23	59	21	19
81–90	7	236	11	0	1	10	17	...	7	28	29
91–100	3	145	4	1	...	10	16	...	...	37	40
101–120	2	51	4	...	...	2	1	...	...	52	44
121–140	...	...	..	...	...	...	..	...	...	3	6
	TAGGED COD RECAPTURED										
	no. %	no. %	no. %	no. %	no. %	no. %	no. %	no. %	no. %	no. %	no. %
41–49	.. ...	0	0 0	.. ....	.. ....	7 25.9	2 15.6	.. ....	.. ....	3	0
50–60	11 5.6	3 3.2	0	17 14.4	53 13.8	28	17	44 55.7	88 32.4	7 22.5	6 15.1
61–70	16 5.7	3	2 3.9	5	24	18 22.5	13 13.8	44 39.9	90	10	8
71–80	5	12 4.4	3	0 10.4	3 15.2	10	7	11	18 34.9	6 20.4	1 6.3
81–90	1 6.8	8 3.4	0 6.7	0	0	3 21.1	2 13.5	.. ....	2	4	2
91–100	0	3 2.6	0	0	.. ....	2	1	.. ....	.. ....	17	8
101–120	0	2	0	.. ....	.. ....	0	0	.. ....	.. ....	12 31.5	7 18.9
121–140	.. ...	.. ...	. ...	.. ....	.. ....	.. ....	.. ....	.. ....	.. ....	0	2

TABLE IIIB. Percentages of tagged cod recaptured in successive years following tagging. For description of the separate tagging experiments A–G, see Table IIIA. (I = internal flat tag; E = bachelor-button opercular tag)

Tagging experiment	A	B	C	D		E		F		G		D, E, F, G	
Method of tagging	E	E	E	I	E	I	E	I	E	I	E	I	E
Year of tagging	1.6	1.7	0.7	7.8	11.0	5.2	6.2	38.2	31.0	5.2	6.5	14.1	13.7
1st year after tagging year	3.5	0.9	2.6	3.6	2.1	10.1	6.9	0.9	1.7	12.6	6.5	6.8	4.3
2nd " " " "	0.4	0.4	0	1.8	0.5	4.2	1.4	2.8	0.6	3.5	0.4	3.1	0.7
3rd " " " "	0	0.2	0	0	0.2	1.4	0	1.8	0.2	1.7	0.4	1.2	0.2
4th " " " "	0.4	0.1	0	0	0.2	1.7	0	1.4	0	1.3	0.4	1.1	0.2
5th " " " "	0	0	0	0	0.2	0.3	0	0	0	0.4	0.4	0.2	0.2
6th " " " "	0	0	0	0	0	0.3	0	0	0	0.4	0	0.2	0
7th " " " "	0	0	0	0	0	0.7	0	0	0	0.4	0	0.3	0
8th " " " "	0	0	0	0	0	0	0	0.5	0	0	0	0	0
10th " " " "	0	0.1	0	0	0	0	0	0	0	0	0	0	0
Number tagged	566	891	153	166	562	286	290	217	587	230	231		
Percentage recaptured, 1st to 10th years after tagging year	4.2	1.8	2.6	5.5	3.2	18.6	8.3	7.4	2.6	20.4	8.1	12.9	5.5
Percentage recaptured, 2nd to 10th years after tagging year	0.8	0.8	0	1.8	1.1	8.6	1.4	6.5	0.8	7.7	1.6	6.1	1.3
Total percentage recaptured	5.8	3.5	3.3	13.3	14.2	23.8	14.5	45.6	33.7	25.7	14.7	27.0	19.3

Total returns were extremely low on the Grand Bank and St. Pierre Bank, 3.5 and 3.3% respectively. On these banks the cod for tagging were all caught by the otter trawl of the *Investigator II* and some of the sets were in water 60–90 fathoms (110–165 m) deep. Almost all the Grand Bank and St. Pierre Bank cod catch was by European vessels. All these factors mitigated against the return of tags.

The low total returns at Englee (5.8%) may be due both to the small amount of cod fishing which occurs in this and neighbouring areas and to the 40–80 fathom (70–150 m) depths at which the fish were caught by linetrawl for tagging.

The returns for the Nutak and Domino areas, 14%, are low because of the relatively small fishing pressure, especially after 1949.

At Corbin and Burin tagging was carried out in the midst of an active cod-trapping area and a very high percentage of the tagged cod was caught in traps several weeks following the tagging. Percentages returned were high — 45.6% for the internal and 33.7% for the external tag — but 38.2% and 31.0% respectively were returned in the tagging year.

Comparison of Bachelor-button Tags with Internal Tags

During the tagging year in 3 out of 4 areas the internal tags gave less returns than the external bachelor-button tags (Table III). We assume that the bachelor-button tags, although lost more readily, are rather more easily seen than the internal tag if the fishermen are not especially looking for tags. In one area, Corbin and Burin, the internal tag gave better returns than the bachelor-button tag in the tagging year. In this area almost all of the large number of returns in the tagging year were obtained from the tagging area within a month after tagging (Fig. 11). The fishermen of the area who were gutting cod were well aware of the possibility that internal tags would be present.The above differences are not statistically significant[1].

In the Nutak-Domino tagging the internal tag gave slightly lower total returns than the bachelor-button external tag but returns of the internal tag were higher than those of the bachelor-button tag for the totals of 1–10 and 2–10 years after the tagging year. None of these differences are statistically significant. (P = 0.9–0.8, 0.3–0.2 and 0.8–0.7 respectively.)

In the remaining 3 areas in which internal and external tags were used χ^2 comparisons showed that the internal tag total returns of 23.8%, 45.6% and 25.7% were significantly higher in each case (P = 0.01–0.001) than the bachelor-button tag returns of 14.5%, 33.7% and 14.7% respectively; and that for the returns for 1–10 and 2–10 years after the tagging year the internal tag returns of 18.6%, 7.4%, 20.4% and 8.6%, 6.5%, 7.7% were usually even more significantly higher (P in 2 cases 0.01–0.001 and in 4 cases < 0.001) than the bachelor-button tag returns of 8.3%, 2.6%, 8.1% and 1.4%, 0.8%, 1.6% respectively.

In all areas where external and internal tags were used, except Corbin-Burin, both types of tags were used in each day's tagging in the same relative numbers

[1]Probabilities (P) for the differences in returns of external and internal tags are from chi-square tests, using 2 × 2 tables under the hypothesis that the returns are independent of the type of tag, and with Yates' adjustment for continuity.

TABLE IV. Recaptures of smaller and of larger cod tagged in the Newfoundland area, 1947–1948. (I = internal flat tag; E = external bachelor-button opercular tag. Cod lengths are snout to mid-fork of the caudal fin.)

Length range	Englee	The Grand Bank[a]	St. Pierre Bank	Nutak and Domino		St. John's		Corbin and Burin		Lark Harbour[a]	
	E	E	E	I	E	I	E	I	E	I	E
cm	NUMBER OF COD TAGGED SUCCESSFULLY										
41–70	478	459	109	159	554	215	216	194	521	110	112
71–140	88	432	44	7	8	71	74	23	66	120	119
	PERCENTAGE OF FISH RECAPTURED IN TAGGING YEAR										
41–70	1.5	1.7	0	8.2	10.8	6.0	6.9	38.1	31.7	1.0	2.7
71–140	2.3	1.6	2.3	0	25.0	2.8	4.1	39.1	25.8	9.2	10.1
	PERCENTAGE FISH RECAPTURED OMITTING TAGGING YEAR										
41–70	4.2	2.2	1.8	5.7	3.1	18.6	7.9	7.2	2.5	22.7	10.7
71–140	4.5	1.4	4.5	0	12.5	18.3	9.5	8.7	3.0	18.3	5.9
	PERCENTAGE RECAPTURED OMITTING TAGGING YEAR AND 1ST YEAR AFTER TAGGING										
41–70	0.6	0.7	0	1.9	1.1	8.8	1.4	6.2	1.0	11.8	2.7
71–140	1.1	1.2	0	0	0	7.0	1.4	8.7	0	4.2	0.8
	PERCENTAGE RECAPTURED OMITTING TAGGING YEAR AND 2 YEARS AFTER TAGGING										
41–70	0.4	0.2	0	0	0.5	5.6	0	4.1	0.2	8.1	1.8
71–140	0	0.7	0	0	0	1.4	0	0	0	0.8	0.8
	PERCENTAGE RECAPTURED OMITTING TAGGING YEAR AND 3 YEARS AFTER TAGGING										
41–70	0.4	0	0	0	0.4	3.7	0	2.1	0	5.5	1.8
71–140	0	0.5	0	0	0	1.4	0	0	0	0	0
	PERCENTAGE RECAPTURED OMITTING TAGGING YEAR AND 4 YEARS AFTER TAGGING										
41–70	0	0	0	0	0.2	1.9	0	0.5	0	2.7	0.9
71–140	0	0.2	0	0	0	0	0	0	0	0	0
	TOTAL PERCENTAGE FISH RECAPTURED										
41–70	5.6	3.9	1.9	13.8	13.9	24.7	14.8	45.4	34.2	23.6	13.4
71–140	6.8	3.0	6.8	0	37.5	21.1	13.5	47.8	28.8	27.5	16.0

[a]The two size groupings used for all cod in these columns were 41–80 cm and 81–140 cm, rather than those shown at left.

as in the totals of each type of tag used in the area. In the Corbin-Burin tagging the favourable effect for the internal tag was obtained despite the fact that internal tags were not available for use until near the end of the tagging — July 6–10 compared with June 19– July 6 for the external tag.

Doubtless many of the bachelor-button tags were lost, even after the tagging year, whereas the internal tags are very unlikely to be lost after the tagging year, and although some may be embedded in organs such as the liver and gonad and become difficult to see as the fish grows larger and the viscera increase in size, they still have a considerable advantage in recovery over the bachelor-button external tag used in our experiment.

Recaptures of Cod of Different Sizes when Tagged

In Tables III and IV there is no consistent trend indicating significant differences in the total recaptures of smaller and of larger cod of the size ranges tagged.

Table IV shows that in the tagging year in some cases the larger and in others the smaller cod gave the highest percentage returns. Beyond the tagging year and the first 2 years after tagging, however, the percentages of tags returned from small cod were greatly in excess of those from larger cod. Evidently the larger cod disappeared from the fishery at a much faster rate than the smaller cod. Natural mortalities of larger cod may be greater, but we suspect that many of these cod are not returning to the normal fishing grounds but are passing to deeper areas (such as those we have discovered off the northeast coast of Newfoundland) where they were not heavily fished.

Effect of Different Methods of Capture for Tagging on Rate of Recapture after Tagging

Cod tagged after they were caught by trap were recaptured fairly regularly by trap immediately after tagging (Table V). Very few other methods of capture were in use in the trapping areas but there was some recapture of these cod by linetrawl and jigger within 2 days after tagging.

Cod caught by handline and linetrawl for tagging at St. John's in the autumn when no traps were operating showed the first recaptures by linetrawl 10 days after tagging. These cod were tagged on 8 separate days, thus unsuitable weather for fishing immediately after the tagging date should not be a very significant factor in the lapse of time between tagging and recapture. There was no obvious difference in time between tagging and recapture for fish caught for tagging by linetrawl or by handline. At Englee, where linetrawled fish were also tagged, the first recapture (by linetrawl) was 7 days after tagging.

McKenzie (1956) says that an inspection of all the recaptures from 2200 cod tagged on 11 different days during 1934–1936 shows that none was recaptured on the day following tagging.

Effect of Depth of Capture of Cod by Otter Trawl for Tagging on Percentage Recapture of Cod

The relatively small number of recaptures shown in Table VI does not demonstrate a relationship between the number of recaptures and the depth at

which the cod were caught by otter trawl for tagging. The average dragging times were similar except at 51–70 fathoms (93–128 m) where the time was considerably greater and no cod were recaptured. Similarly McCracken (MS, 1961) found that over a depth range of 10–60 fathoms (18–110 m) the depth from which cod were taken for tagging did not affect the proportion recaptured.

Effect of Length of Drag in Capturing Cod by Otter Trawl for Tagging, on the Percentage Recaptured

Although the data in Table VII are rather scanty, especially for the 10-minute dragging period, it is evident that there is an inverse relationship between

Table V. Number of days (first 30 days only) from tagging to recapture for cod caught for tagging by trap, by linetrawl and by handline, arranged by type of tag and method of recapture. (H: handline; J: jigger; L: linetrawl; T: trap)

	Tagged after capture by trap (Burin, Corbin, Domino, Nutak)						Tagged after capture by linetrawl (St. John's)			Tagged after capture by handline (St. John's)		
Days after tagging	External tags				Internal tags		External tags	Internal tags		External tags	Internal tags	
	T	L	H	J	T	J	L	L	H	L	L	H
0	4	...	...	...	1	...	...	...	...	...	...	...
1	6	...	...	...	7	...	...	...	...	...	...	...
2	6	1	...	1	8	...	...	...	...	...	...	...
3	1	...	...	1	5	...	...	...	...	...	...	...
4	14	2	...	...	7	...	...	...	...	...	...	...
5	8	2	...	...	9	...	...	...	...	...	...	...
6	13	...	...	1	6	...	...	...	...	...	...	...
7	11	...	...	...	2	...	...	...	...	...	...	...
8	4	...	...	1	6	...	...	...	...	...	...	...
9	5	...	...	...	3	...	...	...	...	...	...	...
10	4	...	...	...	3	...	2	...	...	...	...	...
11	8	...	...	...	3	1	1	1	...	...	1	...
12	3	...	...	...	...	...	1	...	...	...	...	...
13	5	...	...	...	...	...	...	...	...	...	...	...
14	7	...	1	...	3	...	...	1	...	1	...	...
15	3	...	...	...	3	...	...	...	...	...	...	...
16	3	...	...	...	1	...	...	...	1	...	...	...
17	2	...	...	1	1	...	...	...	...	...	...	...
18	5	...	...	...	...	...	...	...	...	...	...	...
19	5	...	...	...	3	...	...	...	...	...	...	...
20	5	...	...	...	...	...	1	...	...	1	1	...
21	6	...	...	...	2	...	...	1	...	...	...	...
22	6	...	...	...	4	...	...	...	...	...	...	1
23	3	...	...	...	2	...	1	...	...	1	1	...
24	8	...	...	1	1	...	...	...	...	...	...	...
25	1	...	...	...	1	...	...	...	...	...	...	...
26	6	...	...	...	...	...	...	...	...	1	...	...
27	1	...	...	...	...	...	...	1	...	...	...	...
28	1	...	...	...	...	...	...	...	...	...	...	...
29	4	...	...	...	...	...	...	...	...	1	...	...
30	5	...	...	...	...	...	...	...	...	...	...	...

TABLE VI. Percentages of tagged cod recaptured after having been caught for tagging in various depth ranges from 20–30 to 71–90 fathoms (37–55 to 130–165 m). Cod were tagged by the *Investigator II* after capture by otter trawl on the Grand Bank, 1947–1948, using bachelor-button tags. (1 fathom = 1.83 m)

Depth of drag	Number tagged	Drag length		Percentage recaptured
		Range	Average	
fathoms		*minutes*	*minutes*	%
20–30	53	45–75	55	1.9
31–40	336	10–90	47	4.5
41–50	491	30–60	47	3.5
51–70	130	30–90	71	0
71–90	63	30–60	45	3.2

the length of the drag from which fish are tagged and the percentage of tagged fish recaptured. There is a steady decline from a 10.3% recapture of fish tagged from 10-minute drags to a 1.0% recapture of fish tagged from 70- to 90-minute drags. In view of the lack of great variation in recapture shown in Table VI at shallow and at greater depths, it is not to be expected that the difference from 32 fathoms (59 m) depth for the 10-minute drags to 42 fathoms (77 m) depth for the 70- to 90-minute drags would produce the differences in percentages recaptured indicated in Table VII.

RECAPTURES OF COD CAUGHT FOR TAGGING BY LINETRAWL AND BY HANDLINE

Table VIII indicates that the handlined cod tagged off St. John's showed a higher percentage recapture than the linetrawled cod. The difference in recaptures was much greater, however, in the year of tagging than in subsequent years. Tagging in St. John's was in the autumn, Oct. 5 to Nov. 4, and the numbers of cod tagged with internal and bachelor-button external tags were approximately equal in each of the following 3 periods, with the number of cod tagged after capture by each method and the percentage recoveries before the end of the year as follows: Oct. 5-11, 118 linetrawled cod tagged, 4% recapture;

TABLE VII. Percentages of tagged cod recaptured after having been caught for tagging by dragging periods from 10 to 70–90 minutes. Cod were tagged by the *Investigator II* after capture by otter trawl on the Grand Bank and St. Pierre Bank, 1947–1948 using bachelor-button tags. (1 fathom = 1.83 m)

Length of drag	No. tagged	Range of depths	Average depth	Percentage recaptured
minutes		*fath*	*fath*	%
10	29	31–33	32	10.3
25–30	308	31–94	46	4.9
45–60	634	29–80	44	2.2
70–90	102	30–53	42	1.0

TABLE VIII. Percentages of tagged cod recaptured after having been caught for tagging by linetrawl and by handline. Cod tagged off St. John's, Oct. 5 to Nov. 4 and Oct. 14–21, 1948.

Dates of tagging	Type of tag	How caught	Number tagged	Percentage recaptured 1948	Percentage recaptured after 1948	Total percentage recaptured
				%	%	%
Oct. 5 to Nov. 4	External	Linetrawl	217	4.6	9.2	13.8
	Internal	"	206	3.9	17.5	21.4
Oct. 14–21	External	Handline	74	10.8	5.4	16.2
	Internal	"	80	8.8	22.5	31.2
Total		Linetrawl	423	4.3	13.2	17.5
		Handline	154	9.7	14.3	24.0

Oct. 14, 30 linetrawled cod tagged, 17% recapture; 18 handlined cod tagged, 22% recapture; Oct. 18-21, 136 handlined cod tagged, 8% recapture; and Oct. 29 to Nov. 4, 275 linetrawled cod tagged, 3% recapture. The handlined cod were obtained in 25–35 fathoms (45–65 m) and the linetrawled cod on a line laid from shallower to deeper water, 30–75 fathoms (55–135 m).

Thus, the first year's data are too variable in time of tagging for adequate comparisons of recaptures of handlined and linetrawled fish to be made. The small advantage of handlined cod for recaptures in the second year is without statistical significance. In our data the linetrawled cod were obtained in flying sets with only about an hour between setting and hauling.

Hansen, Jensen and Tåning (1935) say that experience gained at the Faroes and Iceland has shown that cod taken carefully on handlines are, on the whole, best suited for tagging. In the absence of more detailed information we cannot comment on this statement in relation to our own results.

McCracken (1959 and MS, 1961) had higher returns from handlined than from otter-trawled cod from the Gulf of St. Lawrence. He concluded, however, that the evidence was not good enough to indicate superiority of either of these methods of capture for tagging.

AVERAGE DISTANCES BETWEEN TAGGING AND RECAPTURE FOR COD OF DIFFERENT LENGTHS

The average distances between tagging and recapture locations as shown in Table IX are of actual shortest distances by water between the tagging location and the recapture position. As will be noted in the various figures, even after the tagging year, many more of the cod were usually recaptured near the tagging area rather than distant from it. For any particular size group the distance-recapture frequency is considerably skewed to the right. To obtain a large enough frequency for detailed examination it has been necessary to combine all the inshore frequencies of distances travelled and to combine various length categories (Table X). (The offshore results are too few for detailed examination.) For lack of returns and because the cod gradually grow out of the tagged length groups it has been found necessary to confine the detailed examination to the year after the tagging year.

TABLE IX. Distances (nautical miles) between points of liberation and recapture of cod tagged in inshore and offshore parts of the Newfoundland area, 1947–1948. (Offshore — Grand Bank and St. Pierre Bank. Inshore — Nutak, Domino, Englee, St. John's, Burin and Corbin, Lark Harbour. Recaptures during the tagging year are omitted for the inshore tagging. One nautical mile = 1.85 km.)

Year of recapture	Average recapture distances in nautical miles from tagging area of cod at various cm length groups. Number of fish in parentheses.							Av. recapture distances
	41–50	51–60	61–70	71–80	81–100	101–120	121–140	
	INSHORE TAGGING							
1st year after tagging year	20 (5)	37 (46)	48 (44)	76 (19)	67 (21)	62 (6)	20 (1)	50 (142)
2nd & 3rd years after tagging year	98 (4)	50 (16)	81 (21)	79 (8)	41 (6)	141 (2)	..	71 (57)
4th & 5th years after tagging year	68 (1)	105 (6)	69 (9)	207 (1)	37 (1)	..	..	87 (18)
6th & 7th years after tagging year	35 (1)	117 (3)	122 (1)	..	..	..	..	101 (5)
	OFFSHORE TAGGING							
Year of tagging	..	56 (1)	105 (1)	102 (8)	45 (5)	34 (1)	..	77 (16)
1st year after tagging	..	..	148 (3)	104 (7)	87 (1)	105 (1)	..	114 (12)
2nd, 3rd & 4th years after tagging	..	121 (2)	164 (1)	..	68 (4)	..	..	96 (7)

TABLE X. Minimal distances travelled between tagging and recapture position for cod of three centimetre length-classes, recaptured in the year after the tagging year.

Distance	Number recaptured		
	41–60	81–80	81–140
nautical miles	*no.*	*no.*	*no.*
0–40	38	31	14
41–80	8	16	3
81–120	2	8	2
121–160	1	3	9
161–200	0	4	0
201–240	1	0	0
241–280	1	0	0
281–320	0	1	0
81 up	5	16	11
Total	51	63	28

Chi-square comparisons made on the summary groupings in Table X show that the greater travel distances indicated by the travel frequencies of the 61–80 cm and 81–140 cm groups, compared with that for the 41–60 cm group, are significant ($P = 0.02$ and 0.01, respectively), but that the differences between the frequencies of distances travelled by the 61–80 cm and the 81–140 cm groups are not significant ($P = 0.2$).

If the frequencies of distances travelled by inshore cod in the year after the tagging year are combined in another way, as shown below, χ^2 analysis shows that the greater travel distances indicated by the frequency of distance travelled by the 71–140 cm group compared with that for the 41–70 cm group are highly significant ($P < 0.01$).

Minimal distances of migration	Numbers of recaptured cod	
	41–70 cm	71–140 cm
nautical miles	*no.*	*no.*
0–49	72	23
50–99	13	9
100–up	10	15
Total	95	47

These data are, however, from so many inshore areas and times of tagging, and the differences in sizes of cod tagged in the different areas are such that we cannot have complete confidence in these distance comparisons. More tagging in one area would give better results for the purpose of calculating travel distances. In later years the older fish, of the greatest length when tagged, are not represented in the recaptures.

In the inshore area there is a consistent increase, with time after tagging, in the average minimal distance that the cod has moved from the tagging location.

The distances travelled in any one year are doubtless affected by sexual maturity, with the usual probability that the immature cod migrate smaller distances than the sexually mature cod.

Fleming (1960) indicates that in the Newfoundland inshore area a high percentage of the cod below 60 cm were immature. This is especially true of the female cod while a higher percentage of males of these sizes are sexually mature. Almost all the coastal cod are mature at sizes above 70 cm.

Strubberg (1916), in cod tagging at the Faroes, found the young 2- and 3-year-old cod to be extremely stationary, but older cod, over 60 cm in length, were more migratory. Strubberg (1922) obtained similar results for cod tagged in Danish waters where, for cod marked in the southern Kattegat, most of the fish below 65 cm when tagged were more or less stationary during the first year of the experiment, while those larger than 65 cm quickly moved away from the tagging area.

Hansen *et al.*, (1935), from cod mainly between 50 and 115 cm (37% less than 70 cm, 55% between 70 and 100 cm and 8% over 100 cm) tagged in West Greenland, found that the relatively stationary cod in West Greenland are for the most part either immature or old cod. Of the many cod undertaking the long migration to Iceland the majority belonged to the sizes 70–100 cm. Very few below or above this size range undertake this migration. Many West Greenland cod migrated to Iceland for spawning and very few migrated before they were 8 or 9 years of age. This agrees with the earliest age at which many of these cod were becoming sexually mature.

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Observations on the Isopod *Mesidotea entomon* in the Western Canadian Arctic Ocean[1]

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ABSTRACT

The collection of *Mesidotea entomon* (Linnaeus) during the 1960 cruise of the *Salvelinus* in the western Canadian Arctic ocean has expanded the recorded distribution of the species. Population densities were highest in mud-bottomed areas where water temperatures ranged from −1.3 to +10.0°C. No specimens were collected at depths greater than 24 fathoms (44 m). Sexual dimorphism of *M. entomon* became apparent at lengths of 25 mm, males reaching a larger size than females at maturity in the second year of life. The majority of the population apparently died after reproducing once.

INTRODUCTION

Specimens of the isopod *Mesidotea entomon* (Linnaeus) were collected from the Beaufort Sea during a cruise of the vessel *Salvelinus* operated by the Fisheries Research Board of Canada during the summer of 1960. Collections were made along the coastline extending westward from the Mackenzie Delta nearly to Alaska, particularly in the immediate vicinity of Herschel Island. Some 9776 specimens were collected during the season and 2182 were retained for laboratory study.

M. entomon as described by Richardson (1905) was first named *Idotaega entomon* by Linnaeus (Richardson, 1905) and has been considered to be circumpolar in distribution although information on the distribution and biology of the species is extremely limited. This paper presents details on *M. entomon* not previously described in the literature. Dorsal and ventral views of the species are shown in Fig. 1.

MATERIALS AND METHODS

Specimens of *M. entomon* were collected chiefly by use of an otter trawl which sampled a horizontal strip of bottom approximately 7.5 metres in width. The net ranged from a stretched mesh size of 32 mm in the wings to 13 mm in the cod-end or bag. Quantitative sampling was probably biased towards larger specimens as it was possible for those with lengths of less than 40 mm to pass through the net. Specimens were collected also with a trawl dredge which dug more deeply into the substratum over which it was towed than did the otter trawl.

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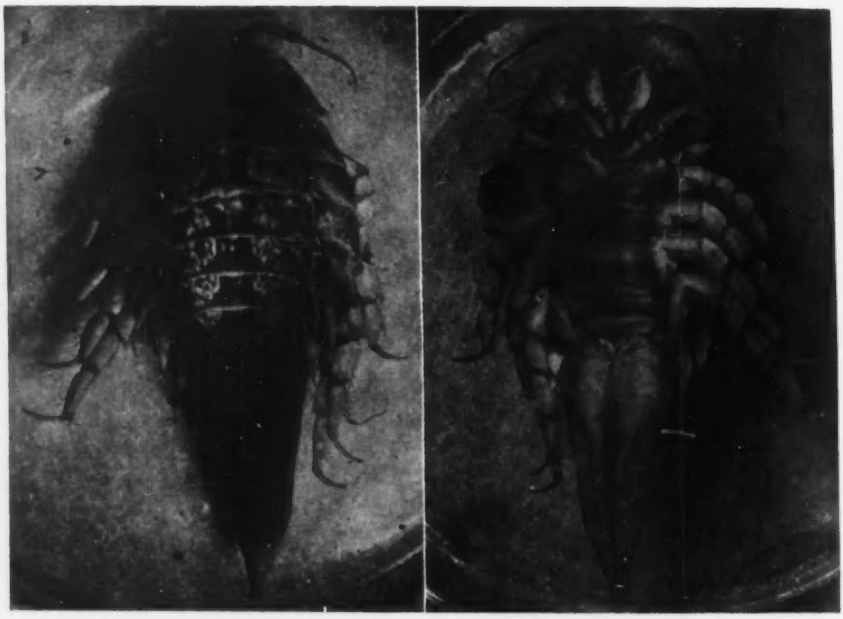

FIG. 1. *Mesidotea entomon*, (a) dorsal, (b) ventral views.

Studies on the anatomy of *M. entomon* were conducted in the Fisheries Laboratory of the Department of Zoology, Ontario Agricultural College.

The length measurement used in describing *M. entomon* is the distance from the end of the telson to the most anterior part of the second article of the second antennae. The second antennae are rigid to this point and a measure of total length can be obtained by flattening the specimen on its ventral surface along a rule.

DISTRIBUTION

Richardson (1905) described the distribution of *M. entomon* as "circumpolar; west coast of North America to Pacific Grove, California; Stockholm's skargard (J. Lindahl); Keilerbucht, Germany; Nakvak, Labrador; Kara Sea".

The Canadian Arctic Expedition of 1913–1918 collected a number of specimens at Grantley Harbour, Point Barrow, Collinson Point, Demarkation Point, and Bartier Island in Alaska, and at Bernard Harbour, Bathurst Inlet, Cape Bathurst, and Banks Peninsula in the Northwest Territories. Many of the specimens were identified from the stomach contents of fish species collected. Boone (1920), in speaking of the findings of the Canadian Arctic Expedition, stated that *M. entomon* was recorded from the Kara Sea, west across polar Europe and America, and the Bering Sea. The Point Barrow study by the United States (MacGinitie, 1955) collected more than 250 specimens which were taken mostly in Eluitkak Pass.

The 1960 study has established the presence of *M. entomon* in previously undescribed locations in the western Arctic. Collections were made in Pauline Cove, Thetis Bay and Simpson and Osborne Points in the immediate vicinity of Herschel Island. Other collections were made at King Point and Shingle Point along the Yukon coast (Table I, Fig. 2).

TABLE I. Catches of *M. entomon* from the western Canadian Arctic by the *Salvelinus* Expedition during August, 1960. ("Numerous" = more than 100 specimens.)

Station Number	Latitude	Longitude	Place	Operation	Catch of *M. entomon*
60–1001	69°32′	138°55′	S of Simpson P.	Otter trawl	numerous
60–1007	69°33′	138°55′	SE Pauline Cove	"	"
	69°33′	138°51′	Pauline Cove	"	"
60–1008	69°33′	138°55′	NE Pauline Cove	"	"
	69°34′	138°54′	N of Herschel I	"	"
60–1009	69°31′	138°50′	SE Pauline Cove	"	740
60–1010	69°31′	138°54′	Osborne Point	"	2182
60–1011	69°33′	138°51′	Pauline Cove	Small trawl	numerous
60–1012	69°30′	138°51′	Simpson Point	"	"
60–1014	69°34′	139°18′	W of Herschel I.	Otter Trawl	859
60–1015	69°36′	139°17′	W of Herschel I.	"	466
60–1016	69°37′	139°57′	W of Herschel I.	"	268
60–1021	69°31′	139°05′	NE Osborne P.	"	1516
60–1022	69°34′	138°51′	N of Herschel I.	"	numerous
60–1023	69°33′	138°51′	Pauline Cove	Small trawl	"
60–1025	69°33′	138°51′	Pauline Cove	Trawl dredge	"
60–1027	69°33′	138°51′	Pauline Cove	Small trawl	"
60–1029	69°33′	138°51′	Pauline Cove	Otter trawl	"
60–1035	69°32′	138°57′	Thetis Bay	"	2517
60–1036	69°32′	138°57′	Thetis Bay	"	1228
60–1042	69°06′	137°55′	King Point Harbour	Trawl dredge	few
60–1043	69°08′	137°55′	N of King P.	Otter trawl	"
60–1044	69°00′	137°23′	Shingle Point	Hand seine	"

M. entomon was found to live as a scavenger on the sea bottom where it ate a variety of animal remains although large specimens were observed occasionally to have preyed upon such organisms as Euphausiacea. Although Boone (1920) noted that the young of *M. entomon* were pelagic, no evidence of this was attained in the present study.

An analysis of August otter trawl haul collections (Table II) indicated that the population density was highest in mud bottomed areas (0.46–0.93 g/m^2), lowest in sand and gravel areas. Trawl hauls in water deeper than 24 fathoms failed to capture any of the species, which supports the suggestion of MacGinitie (1955) that *M. entomon* may prefer shallow water. *M. entomon* was collected in water with temperatures ranging from -1.3 to $+10.0$°C; this wide range in water temperature in the Herschel Island area was caused by the influence of the Mackenzie River.

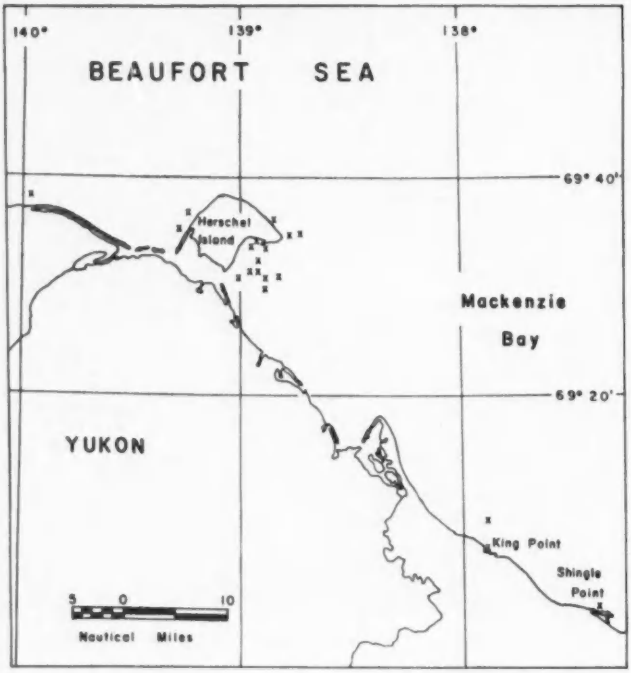

FIG. 2. Locations of captures of *Mesidotea entomon* in the western Arctic Ocean, 1960.

TABLE II. Data on specimens of *M. entomon* collected in otter-trawl hauls, August, 1960.

Station number	Date	Water depth	Bottom temp.	Bottom type	Collections of *M. entomon*	
					Number	Density
		fathoms	°C			g/m^2
60–1009	August 2	10–15	−1.2	mud	740	0.46
60–1010	August 3	4–6	−0.5	mud	2182	0.75
60–1014	August 6	2	+4.1	gravel	859	0.21
60–1015	August 6	2	+7.6	gravel	466	0.18
60–1016	August 6	7	+0.9	gravel and stone	268	0.09
60–1021	August 10	3–5	+1.6	gravel and sand	1515	0.38
60–1035	August 25	12–24	−1.3	mud	2517	0.96
60–1036	August 25	20–21	−1.3	mud	1228	0.66

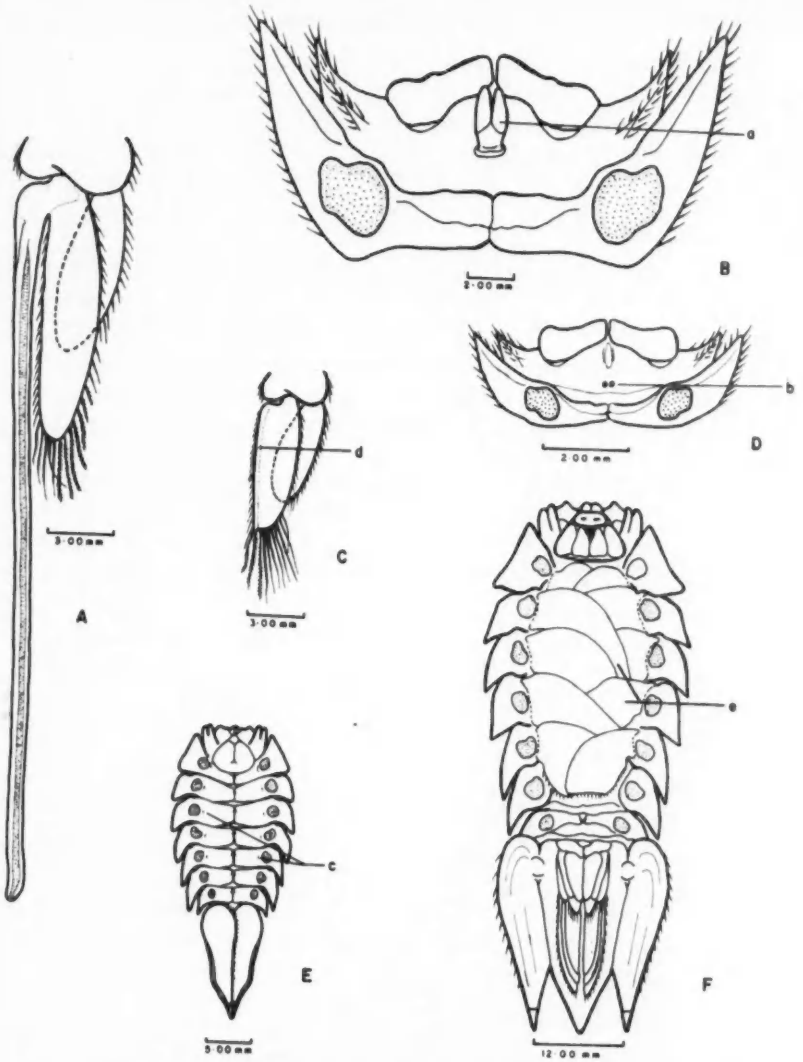

FIG. 3. Sexual dimorphism in *Mesidotea entomon*, male and female
A. Copulatory style on endopodite of second pleopod of mature male.
B. Ventral surface of 7th thoracic segment of mature male showing paired penes (a) projecting caudally.
C. Precursor of copulatory style (d) appearing on endopodite of second pleopod of immature male (total length 30 mm).
D. First appearance of paired penes (b) on ventral surface of 7th thoracic segment of immature male (total length 30 mm).
E. Rudiments of oostegites (c) appearing on mesal margins of coxae of pereiopods 1–5 on immature female (total length 35 mm).
F. Fully developed oostegites (e) overlapping to form brood pouch on ventral surface of mature female.

SEXUAL DIMORPHISM

Sexual dimorphism becomes apparent in *M. entomon* at a total length of about 25 mm. Tiny projections originating from the mesal margins of the coxae of the first 5 thoracic segments begin to appear on the ventral surface of the thorax of females. An accelerated development of these structures takes place at a length of 50 to 75 mm when the females are approaching maturity. The large, overlapping oostegites formed thereby serve as a brood pouch in which the ova develop (Fig. 3E, F).

The ova pass into the brood pouch through genital ducts which open on the ventral surface of the fifth abdominal segment. One genital duct appears on each of the lateral edges of the segment close to the points of attachment of the

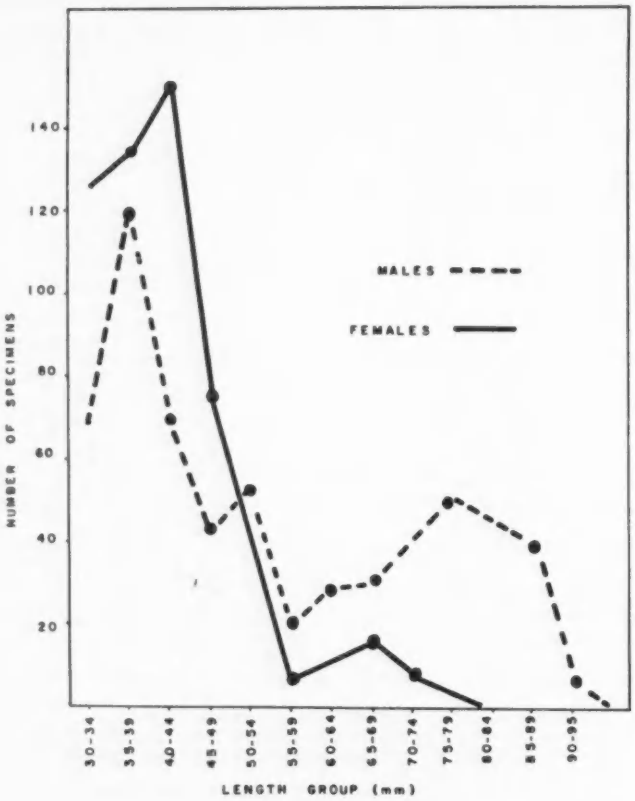

FIG. 4. Length frequency curves for *Mesidotea entomon* taken in otter trawl hauls, August, 1960.

oostegites. These genital ducts extend into the body cavity and end in sort of fimbria. Ova are transported through the ducts and remain unattached within the cavity created between the ventral wall of the abdomen and the overlapping oostegites. Here the ova develop to a length of 3–5 mm at which time they drop into the water as free-living individuals.

Male specimens show a continuous sexual development which is readily observed after specimens reach total lengths of about 25 mm. A pair of penes develop in the middle of the ventral surface of the 7th thoracic segment and, at maturity, project caudally (Fig. 3B, D). At an early stage also, a projection appears at the distal end of the endopodite of the second pleopod on the side nearest the mid-line.

This projection gradually lengthens and separates from the endopodite until it forms a sort of style hinged to the endopodite at the base only by the time the animal reaches maturity. (Fig. 3A, C). The styles appearing on the paired second pleopods adjoin one another along their entire lengths. Because the adjoining styles are grooved, they form a functional tube which, in mature specimens, extends to the end of the telson and would appear to have a copulatory function. Males with fully-developed copulatory styles were considered to be mature.

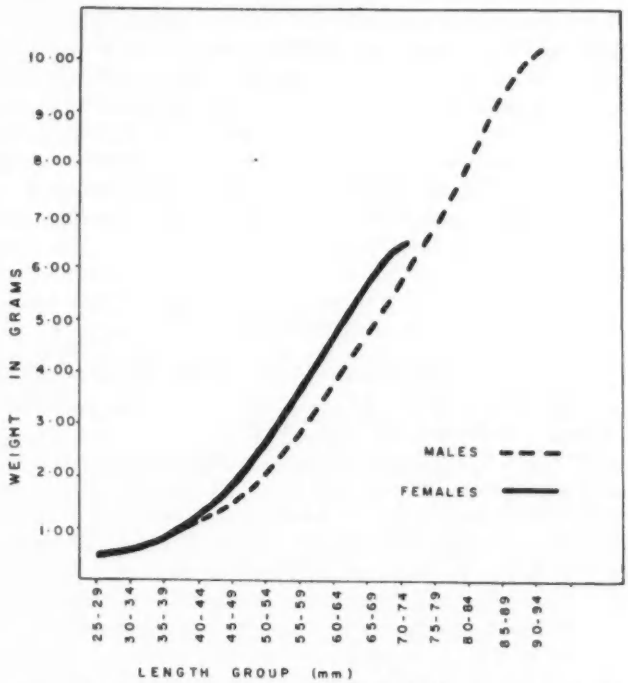

FIG. 5. The length–weight relationship for *Mesidotea entomon* taken in otter trawl hauls, August, 1960.

AGE AND MATURITY

Although no satisfactory method was established for determining the age of *M. entomon*, the length frequency curves obtained from an analysis of the 2182 specimens collected in one haul at a depth of 4–6 fathoms (Station 60–1010) on August 3, 1960, showed two peaks suggesting two age groups (Fig. 4). An examination of the two groups showed that specimens of less than 50 mm in total length were immature young-of-the-year. Mature females ranged from 50 to 79 mm, males from 65 to 95 mm.

Growth curves determined by the examination of 275 preserved specimens (Fig. 5) revealed a similar increase in weight per unit length for both sexes until a total length of 40 mm was reached. At greater lengths, females increased in weight more rapidly than males because of the development of the ovaries. Spent females in the 75–80 mm range caused a fall-off in the growth curve for that sex. Males grew to a greater length than did the females and exhibited a fall-off in the growth curve in the 90–95 mm range because of the physiological degeneration.

Present findings suggest that the majority of *M. entomon* die after reproducing once. The digestive tracts of spent females and large males almost invariably lacked food, the exoskeleton appeared soft, and the internal organs became degenerate. However, the presence of miniature ova (with a diameter of about 0.25 mm) within the body cavity of two spent females among the large number examined suggests that some females may be capable of completing more than one reproductive season. During June, July and August of 1960, mature females ranged in condition from those containing from 285 to 497 small yellow-green, irregular ova within their brood pouches to those which were in the spent condition. Thus the development of ova and deposition of young appeared to be continuous throughout the Arctic summer.

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On the Fecundity of Pacific Cod (*Gadus macrocephalus* Tilesius) from Hecate Strait, British Columbia[1]

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ABSTRACT

Egg counts were made on 46 mature female cod. A log-log relationship was established between egg number and body length. It was shown that there is little difference in the number of eggs per unit body length, between cod from Hecate Strait and stocks from colder regions of the Pacific to the north and west. A comparison of the modal size of mature fish from Hecate Strait and West Kamchatka shows that the former mature at a much smaller size. Since egg number is related to size, it is concluded that the cod stocks of Hecate Strait have a much lower reproductive potential than do other populations in the North Pacific.

INTRODUCTION

The Pacific cod (*Gadus macrocephalus* Tilesius) grows more rapidly, matures earlier, and has a shorter life span in waters along the Canadian coast than in colder regions of the Pacific to the north and west (Ketchen, 1961). Ketchen concluded that, if the relationship between body length and fecundity within the species is constant, the reproductive capacity of Canadian cod per unit number of spawners is about half that in the region of Kamchatka. Left unsatisfied was the assumption that egg number at a given weight of fish (or ovary) is constant within the species, for Moiseev (1953) had presented fragmentary evidence to the contrary, regarding the cod of the northwestern Pacific. Thus there remained the possibility that the smaller average size of mature fish in Canadian waters was compensated for by a smaller size of egg, and hence by a larger number of eggs per unit of body (or ovary) weight.

PROCEDURE

In 1961 a study was made of the fecundity of Pacific cod in Hecate Strait, British Columbia. During a February tagging trip to the White Rock spawning ground (53°35′N, 135°45′W), ovaries were removed from 50 mature or maturing cod, and preserved in 10% formalin. In the laboratory the eggs were removed manually from the ovarian membranes and washed. Connective tissue was removed by sieving and successive decanting. The eggs were then partially dried and sub-samples of from 1,000 to 10,000 eggs (depending on the size of the ovary) were counted under a binocular microscope. The sub-samples and the remainder of the eggs were then fully dried in an electric oven to constant weight

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(approximately 48–60 hours at 65–70°C) and then weighed. The total number of eggs was calculated by direct proportion. Four samples were rejected as being spoiled or insufficiently mature.

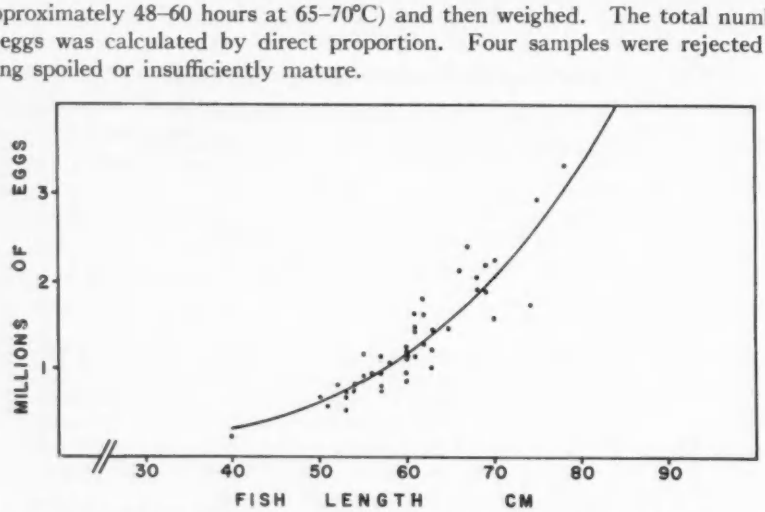

FIG. 1. Fecundity of Pacific cod from Hecate Strait. The solid line is the calculated regression: $\log_{10}$ fecundity (in thousands) = 3.64658 $\log_{10}$ fish length (in cm) − 3.41209

TABLE I. Length and fecundity (number of eggs) of Pacific cod from Hecate Strait

Length	Fecundity	Length	Fecundity	Length	Fecundity
cm	*thousands*	*cm*	*thousands*	*cm*	*thousands*
40	228	57	1,164	63	1,214
50	655	58	1,073	63	1,417
51	587	60	1,212	65	1,468
52	837	60	1,139	66	2,147
53	531	60	1,210	67	2,396
53	686	60	889	68	2,069
53	740	60	1,250	68	1,901
54	749	60	996	69	2,220
54	826	61	1,155	69	1,922
55	889	61	1,492	70	2,256
55	1,170	61	1,434	74	1,757
55	917	61	1,626	75	2,969
56	944	62	1,832	78	3,329
57	748	62	1,306	88	3,215
57	799	62	1,624	...	...
57	974	63	1,020	...	...

RESULTS

The counts obtained are given in Table I and plotted in Fig. 1.

A log-log regression line was fitted to the data. The formula for the line was:

$$\hat{Y} = 3.64658X - 3.41209$$

where "$\hat{Y}$" is $\log_{10}$ of fecundity expressed in thousands of eggs, and "X" is $\log_{10}$ of fish length expressed in centimetres.

Moiseev (1953) has summarized most of the available data on the fecundity of the Pacific cod with particular reference to the western shores of the Pacific

Ocean. Figure 2 illustrates the relationship between the Hecate Strait cod, and stocks on the western side of the Pacific with respect to fecundity. This figure suggests that within the length range studied (40–88 cm) there is no difference in the production of eggs in proportion to body length between the cod of Hecate Strait and those of West Kamchatka. There is a suggestion that cod from Sakhalin produce a greater number of eggs per unit of body length than the cod of West Kamchatka or Hecate Strait. However, the data in support of this difference are extremely scanty (12 specimens from Sakhalin, 10 from Kamchatka). Moiseev also makes a brief reference to the fecundity of cod from the region of Hokkaido stating that it runs from 1,500,000 to 3,000,000 for fish 60 to 90 cm long. This is very close to the results obtained for Hecate Strait cod. Discounting the higher fecundity of the cod of Sakhalin as being due to insufficient sampling, there is no basis to dispute Ketchen's assumption, stated above, that the fecundity-length relationship for the species is constant.

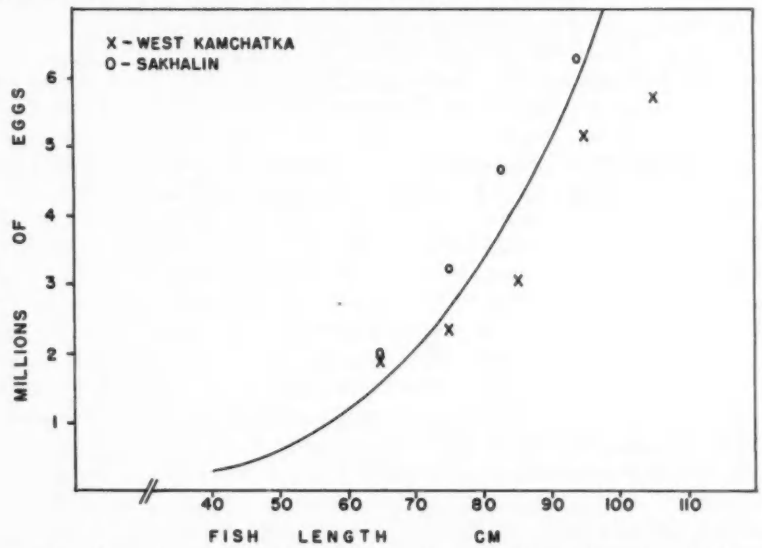

FIG. 2. Comparison of fecundity of Pacific cod from Hecate Strait as calculated from Table I (solid line), with average figures from two stocks of the northwestern Pacific Ocean.

SIZE AT MATURITY

Moiseev (1953) presents data for the cod of West Kamchatka which show that 50% of the females reach maturity at about 73 cm. An analysis of samples from commercial landings combined with samples taken while tagging during the spawning period in 1960 and 1961 shows that 50% of the female cod from Hecate Strait are mature at a length of about 55 cm. A similar situation exists with male cod. Moiseev's data yield a 50% mature length of 69 cm for male cod of West Kamchatka, while in Hecate Strait, 50% of male cod are mature at length of 50 cm. Figure 3 illustrates these relationships.

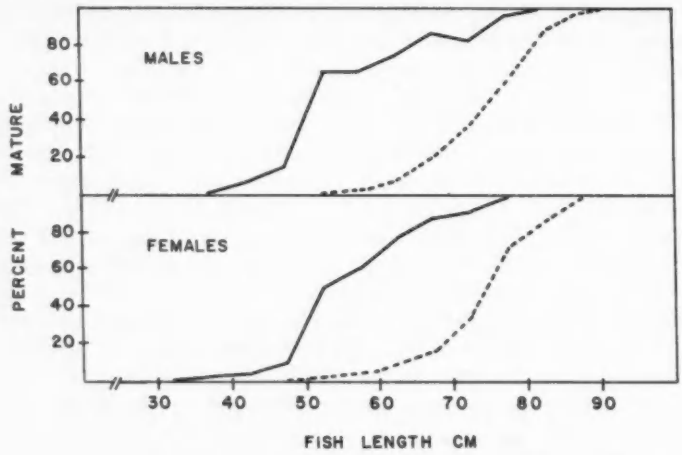

FIG. 3. Comparison of percentage mature cod between Hecate Strait (solid line) and west Kamchatka (broken line).

Accordingly, since both stocks produce roughly the same number of eggs at a given body length (as shown above), the cod stock of West Kamchatka has a higher reproductive potential than the cod of Hecate Strait. This can easily be shown by a simple calculation. The modal frequency of mature female cod from West Kamchatka is about 80 cm, in comparison to 60 cm for Hecate Strait. Using Moiseev's data, Ketchen (1961) calculated that 1000 mature female cod from west Kamchatka would produce approximately 2.93×10^9 eggs. An equal number of cod from Hecate Strait would produce about 1.38×10^9 eggs, or approximately half the number of eggs for an equivalent number of spawners.

Comparisons with the Atlantic cod (*Gadus morhua*) are virtually impossible to make since the specimens of that species which have been examined were almost invariably larger than any studied in this presentation. Nevertheless, there is some evidence suggesting that, in relation to body size, the Atlantic cod has a lower fecundity than the Pacific cod. However, the larger modal size of the spawning stock more than compensates for the lower fecundity. Moiseev considers the Atlantic cod stock to have a higher reproductive potential than the cod of West Kamchatka. This, then, would place the Hecate Strait stock well down on any scale of reproductive potential.

Acknowledgement is made to Miss Sandra Shaw for her assistance in counting the eggs.

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The Periodicity of *Melosira islandica* O. Müll. in Great Slave Lake[1]

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Shortly before his death, Professor D. S. Rawson asked me to examine some samples of net plankton from certain Canadian lakes and discussed their qualitative composition with me. In most of the samples from the Great Slave Lake a heavily silicified form of *Melosira islandica* was dominant. The results of an investigation on a much more delicate species of *Melosira* (Lund 1954, 1955) suggested that the periodicity of *M. islandica* in Great Slave Lake would be much affected by turbulence. In certain lakes in the English Lake District, the periodicity of *M. italica* (Ehr.) Kütz. subsp. *subarctica* O. Müll. in the plankton is directly related to thermal stratification. Its rate of sinking is such that when the water stratifies in summer the population passes rapidly into the hypolimnion and so on to the deposits. There a large part of the crop remains alive until re-suspended during the antumnal circulation (Lund, 1954). If ice-cover is prolonged similar changes take place. The changes under ice in the Great Slave Lake are not known but a considerable number of cell counts were made by Rawson after the break-up of the ice and in the three succeeding months. Allowance must be made for the difficulty of obtaining accurate quantitative data from net hauls. Nevertheless it is probable that the differences between the sizes of the crops during summer were greater, not smaller, than Rawson found. His results are very striking.

Species of *Melosira* are, at times, abundant in other Canadian lakes and it is reasonable to expect that this genus is one of the main producers of food for animals in many lakes in Canada, particularly those in the north. Therefore, either directly or indirectly, it is important for fisheries. Professor Rawson had the success of the inland fishery industry very much at heart and made many valuable contributions to problems concerned with it as well as making substantial contributions to continental limnology in general. This paper is, therefore, a small contribution to one side of his work and is written in his memory and honour.

The approximate periods when direct thermal stratification started in the Great Slave Lake between 1946–54 can be found from Rawson's figures 7–9 (Rawson 1956). These periods are shown in Fig. 2 in relation to the date of collection of the sample with the largest number of *Melosira* in it. There is a clear relationship between the timing of the onset of thermal stratification and that of the maximum of *Melosira*. When, moreover, average values for his

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Melosira counts and for the date of the assumption of thermal stratification for 1946–54 are plotted (Fig. 1-3), this relationship is seen even more strikingly. Further, it has to be remembered that the counts were made on vertical hauls. The depth at the station concerned (no. 31) is 140 m and the hauls were taken from close to the bottom up to the surface. Therefore, large numbers of *Melosira* will still be collected after it has begun to sink out of the upper, photic layers in which photosynthesis, and so growth, are possible. The true dates of the maximal growth of *Melosira* will certainly be earlier than those recorded and this is the reason why the time of the maximum crop he caught is slightly earlier than the average time of the beginning of stratification (Fig. 1). Figure 3 is drawn from the data in table 10 of Rawson (1956, p. 100). The water at this station (no. 36) is over 600 m deep, yet the decrease in *Melosira* in one month after the approximate start of thermal stratification (see Fig. 2) is very large. This again suggests that the rate of sinking is rapid once turbulence is reduced in the water column as a whole.

The time of the return of *Melosira* cannot be determined because only once was a sample taken apparently during the isothermal autumnal period. This was on September 1st 1953 and conditions were clearly abnormal. Though the air temperature was still high the water was approximately 5°C, after being 17°C at the surface two weeks earlier. It is difficult to see how such a change to complete isothermy can have taken place without extraordinary winds unless seiche movements were involved. The position of station 31 (Rawson, 1956, fig. 1) is such that it lies at the northeast end of the main stretch of open water. It is then probable that the change on September 1st represents upwelling of cold hypolimnion water at the end of a seiche axis some 190 km long, and not the overturn of the lake. If this was so then the general decrease in the plankton as a whole (Rawson, 1956, table H) is explicable and no marked increase in the numbers of *Melosira* would be expected. The evidence from other years suggests that *Melosira* usually was increasing slightly by the time the last samples were taken and when the temperature was falling. The changes are, however, too small for any certainty on this point.

It is clear (Fig. 1; and Rawson, 1956, p. 80) that large crops of *Melosira* arise soon after ice-cover is lost. This suggests that *Melosira* either grows very rapidly at the still low temperatures or that the crop is partially composed of cells which have passed the winter on the deposits. Rawson's data, therefore, supports the view that the cycle of *M. islandica* in the Great Slave Lake is as intimately bound to the changes in the vertical distribution of water density, and so of turbulence, as is that of *M. italica* subsp. *subarctica* in the English Lake District. It will be of interest to see if species of *Melosira* predominate in the plankton of lakes even further north, for example those which are frozen continuously for a year or more. Great Bear Lake would provide an interesting comparison.

In view of the interesting data collected by Rawson while considering other problems, it is to be hoped that estimations of phytoplankton will be included in the programme of fishery research in the Canadian arctic.

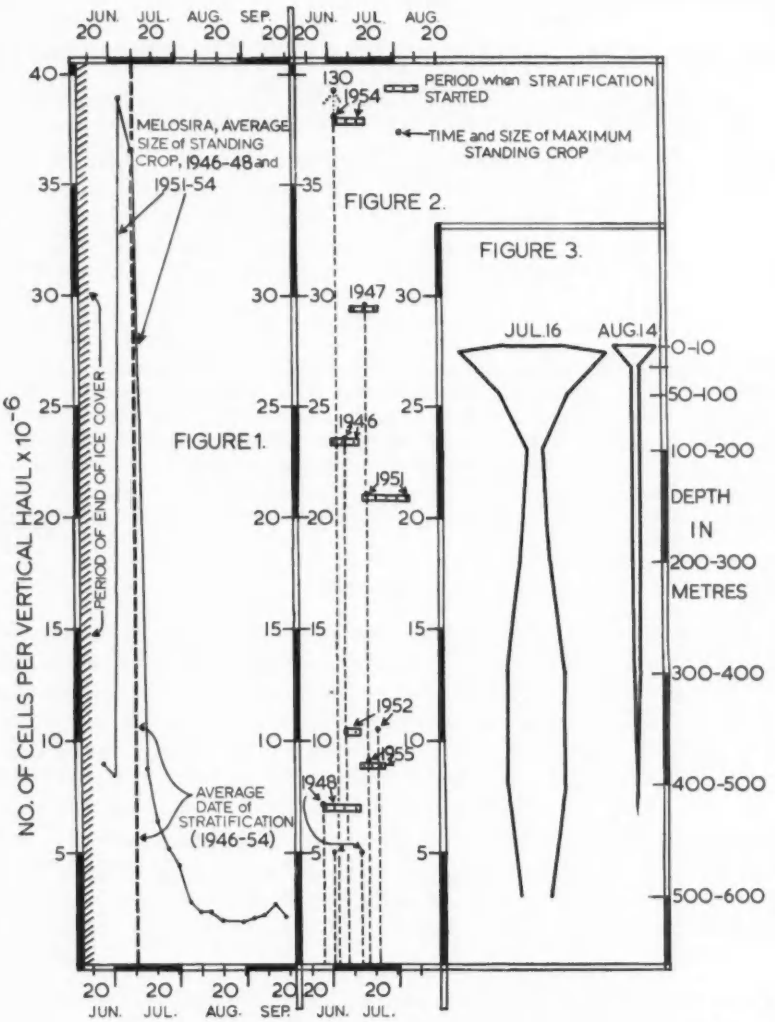

FIG. 1. Mean standing crop in relation to the average date for the onset of thermal stratification for the years 1946–54 inclusive.

FIG. 2. Yearly dates of the maximum observed crop of *Melosira* and of the period in which thermal stratification arose. In 1948 the crop was of similar size for about 3 weeks so that 3 records are shown. The crop in 1954 was over 4 times larger than any other.

FIG. 3. Relative abundance of *Melosira* in depth at station 36, on July 16th and August 14th 1947 (numbers per net haul). Other explanations on the figures. All figures are constructed from data of Rawson (1956).

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Biosynthesis of Trimethylammonium Compounds in Aquatic Animals
III. Choline Metabolism in Marine Crustacea[1]

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ABSTRACT

The incorporation *in vivo* of radioactivity into phospholipid-bound choline has been studied in lobster (*Homarus americanus*) following intramuscular administration of Na-formate-C^{14}, glycine-2-C^{14}, DL-serine-3-C^{14}, L-methionine-methyl-C^{14} and choline-methyl-C^{14}. Choline and methionine were utilized for formation of phospholipid choline at both metabolic periods of 24 and 72 hours, whereas the other compounds gave only a very limited labelling.

When choline-methyl-C^{14} was administered to crab (*Cancer magister*), after 24 hours 1.9% of the administered radioactivity was found in phospholipid choline and 0.1% in trimethylamine oxide.

INTRODUCTION

In the previous studies of this series, tracer experiments conducted with living lobster have shown that choline is a precursor of betaine and trimethylamine oxide (Bilinski, 1960). It was also observed that the oxidation of choline to betaine is not likely to be an intermediate step in formation of trimethylamine oxide (Bilinski, 1961). In connection with the role played by choline in the biosynthesis of other trimethylammonium compounds, it was thought desirable to gain information on the formation of choline in lobster.

In the present study the incorporation of radioactivity into phospholipid-bound choline is investigated after administration to lobsters of C^{14}-labelled compounds known to be associated with the intermediary metabolism of the methyl group. A study of utilization of choline-methyl-C^{14} by the crab is also reported.

EXPERIMENTAL MATERIALS AND METHODS

American Lobster (*Homarus americanus*)

The formation of phospholipid choline in lobster was studied using the material collected during a previous series of experiments dealing with the formation of trimethylamine oxide and betaine (Bilinski, 1960)[2]. This material consisted of the residues from the trichloracetic acid extraction of the combined

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[2]These experiments were conducted on the Atlantic coast at the Fisheries Research Board of Canada Technological Station, Grande-Rivière, Quebec.

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internal organs, muscle and body fluids used in experiments in which C^{14}-labelled compounds, listed in Table I, were administered to lobsters by injection into the abdominal muscle. The animals were sacrificed at the end of a metabolic period of 24 and 72 hours. Details of the administration of labelled compounds were given previously.

Edible Crab (*Cancer magister*)

Crabs were caught in English Bay, Vancouver, B.C. Choline-methyl-C^{14}-chloride (New England Nuclear Corp.) was injected with a clinical needle into each side of the body between the first and second legs. After a metabolic period of 24 hours, the whole body including the carapace was subjected to trichloracetic acid extraction.

Isolation of Phospholipid-bound Choline

The residue from the trichloracetic acid extraction was thoroughly washed with trichloracetic acid 5% (w/v). It was extracted with several portions of boiling ethanol and then extracted with ethyl ether in a Soxhlet extractor. The combined ethanol and ether extracts were evaporated *in vacuo* to near dryness and the residue was extracted with ether. The procedure of du Vigneaud *et al.* (1941) as described by Stekol (1957) was employed for isolation of choline from the ether extract. The choline reineckate was converted to choline chloride by the ion exchange method of Arnstein (1960). The purity of the isolated choline chloride was confirmed by paper chromatography. The modified Dragendorff solution (Bregoff *et al.*, 1953) and 0.2% ninhydrin in 95% ethanol (Block *et al.*, 1952) were used for developing of chromatograms.

Table I. Utilization of C^{14}-labelled compounds for biosynthesis of phospholipid-bound choline in lobsters.

Expt. No.	Weight of lobsters	Metabolic period	C^{14}-labelled precursor	Amount administered per 100 g body weight*	Specific radioactivity of phospholipid choline
	grams	*hours*		*micromoles*	*counts per minute***
1	320 and 358	24	Sodium formate-C^{14}	0.50	<5
2	388 and 305	72	Sodium formate-C^{14}	0.50	<5
3	353 and 351	24	Glycine-2-C^{14}	0.54	Nil
4	390	72	Glycine-2-C^{14}	0.54	<5
5	410 and 518	24	L-methionine-methyl-C^{14}	0.37	115
6	439	72	L-methionine-methyl-C^{14}	0.37	150
7	294 and 500	24	DL-serine-3-C^{14}	0.23	<5
8	410 and 460	72	DL-serine-3-C^{14}	0.23	<5
9	407	24	Choline-methyl-C^{14} chloride	0.84	1450
10	367	72	Choline-methyl-C^{14} chloride	0.84	1750

* A uniform amount of radioactivity (2 μ curies per 100 g body weight) was given with each of the compounds.

** Per infinitely thick planchet (3.8 sq cm) of $BaCO_3$.

Isolation of Trimethylamine Oxide

Trimethylamine oxide was isolated from the trichloracetic acid extract of crab by means of ion exchange chromatography as previously described (Bilinski, 1960). The procedure employed is a slight modification of the method developed by Friedman *et al.* (1955).

Determination of Trimethylamine Oxide

For quantitative determination of trimethylamine oxide in crab, an aliquot of three combined extractions with trichloracetic acid 5% (w/v) was used. Trimethylamine oxide was reduced to trimethylamine with Devarda alloy by the method of Norris and Benoit (1945a). Trimethylamine was estimated by the Beatty and Gibbons (1937) modification of the microdiffusion technique of Conway and Byrne (1933).

Determination of Radioactivity

All compounds were converted to $BaCO_3$ and counted at infinite thickness, as previously described (Bilinski, 1960).

RESULTS AND DISCUSSION

The results of the experiments with lobsters are presented in Table I. As indicated by the experiments with choline-methyl-C^{14}, the administration of free choline to lobster resulted in its incorporation into phospholipids. The enzymic mechanism for the incorporation of choline into lecithin is now well established (Kennedy, 1957). This process involves as a first step the phosphorylation of choline at the expense of adenosine triphosphate, followed by synthesis of cytidine diphosphate choline from cytidine triphosphate and phosphoryl choline. This coenzyme form of choline reacts with a 1,2-diglyceride to form a lecithin.

Regarding the biosynthesis of choline, it is known that the methyl group for its formation may be supplied either in preformed state as methionine or by *de novo* synthesis via a folic acid derivative. As indicated in Table I, in lobster methionine-methyl-C^{14} was utilized for the formation of phospholipid-bound choline. Such a reaction involves the activation of methionine by adenosine triphosphate (Cantoni, 1955). The resulting S-adenosyl methionine serves as a donor of the methyl groups for methylation of ethanolamine. Recently evidence was presented that phospholipid choline is formed by stepwise transfer of three methyl groups from S-adenosyl methionine to phosphatidyl ethanolamine, rather than to other forms of ethanolanine (Bremer *et al.*, 1960; Bremer and Greenberg, 1961; Gibson *et al.*, 1961). In the previous communication of this series the incorporation of tracer into betaine and trimethylamine oxide after administration of methionine-methyl-C^{14} to lobster was attributed to the participation of methionine in the formation of choline (Bilinski, 1960). The observed incorporation of methyl groups of methionine into phospholipid choline supports this intepretation.

The *de novo* synthesis of the methyl groups of choline from compounds related to the biologically active one-carbon fragment could not be demonstrated in the present investigation. This is indicated by the absence of any appreciable labelling in choline after administration to lobster of formate-C^{14}, glycine-2-C^{14} and serine-3-C^{14}. It was previously observed in other studies on invertebrates that formate is not used to any appreciable extent for the formation of methyl groups (Hultin, 1957; Hodgson *et al.*, 1960). The experimental technique employed in the present investigation, however, provides no conclusive evidence for the metabolic deficiency of lobster in regard to the *de novo* synthesis of the methyl groups of choline, as it is known that in animals this process is dependent on a dietary supply of vitamin B_{12} and folic acid (Meister, 1957). Recently several enzymes concerned with other biological reactions of one-carbon derivatives of folic acid were demonstrated in the tissue of invertebrates (Whiteley, 1960).

The results of experiments conducted with crab are presented in Table II. Choline-methyl-C^{14} was the only compound administered. The metabolic pathways of choline observed in experiments with lobster were conversion of choline to betaine and trimethylamine oxide, and its incorporation into phospholipids. However, the present data indicate the occurrence in crab of only the last two of these pathways, as insufficient betaine was found to permit measurement of its radioactivity. The values for the percentage conversion of choline-methyl-C^{14} (Table II) are expressed on the basis of amounts of administered choline and of trimethylamine oxide and phospholipid choline present in crabs at the end of the experiment. These values are minimal ones only, as no allowance was made for the radioactivity eliminated from the body during the experimental period. These experiments confirm the earlier observation made with lobsters that choline may serve as a precursor of trimethylamine oxide. Trimethylamine is the most likely intermediate in this process and it is well established that the oxidation of trimethylamine to trimethylamine oxide takes place in animals (Baker and Chaykin, 1960).

TABLE II. Utilization of choline-methyl-C^{14} in crab.*

Isolated compound	Amount present per 100 g body weight	Specific radioactivity	Percent of total radioactivity
	millimoles	*counts per minute***	
Trimethylamine oxide	0.45	120	>0.1
Phospholipid choline	0.07	8800	>1.9

* 2.7 μ curies as 3.5 μM choline-methyl-C^{14}-chloride was administered per 100 g body weight. Two crabs (total weight 184 g) were sacrificed after a metabolic period of 24 hours.
** Per infinitely thick planchet (3.8 sq cm) of $BaCO_3$.

The ability of animals to convert choline to trimethylamine has been the object of several studies. In mammals the conversion of choline to trimethyl-

amine has been attributed to microbial activity in the digestive tract (Norris and Benoit, 1945b; Huerga and Popper, 1951, 1952; Huerga *et al.*, 1951, 1953) or to an enzymic system in the animal (Artom and Cowder, 1950; Artom and Lofland, 1955; Riedesel and Hines, 1953; Rohse and Searle, 1955; Nakayama and Johnston, 1959). Recently, Prentiss *et al.* (1961). demonstrated that in the rat microorganisms are chiefly responsible for the formation of urinary trimethylamine following administration of choline by stomach tube. They noted, however, that in germ-free rats the conversion of choline to trimethylamine was not completely suppressed. In our experiments an attempt was made to eliminate the interference from microbial flora by avoiding the digestive tract during the administration of the labelled compounds and the results suggest the presence in both species under study of an enzyme system capable of converting choline to trimethylamine oxide. It is felt, however, that further evidence is required to establish if this pathway is of major importance in the accumulation of trimethylamine oxide in marine crustacea. In the other forms of marine animals there is no evidence for a metabolic pathway for synthesis of trimethylamine oxide (Groninger, 1959), although there is indication for its endegenous origin in some species of marine fish (Okaichi *et al.*, 1959).

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OBITUARY

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Alexander Henry Leim

1897 — 1960

Dr. Alexander Henry Leim, senior scientific member in years of service on the staff of the Fisheries Research Board of Canada, died on December 15th, 1960. A son of Henry and Janet (Anderson) Leim, he was born at Fergus, Ontario, November 10th, 1897. Completing his earlier education at local schools he attended the University of Toronto, receiving the B.A. degree and in 1924 the degree of Doctor of Philosophy in marine biology. He became associated with the Biological Board of Canada (now the Fisheries Research Board of Canada) in 1919, when as a seasonal investigator at the Atlantic Biological Station he initiated a study of the life history of the shad, with particular reference to the factors responsible for a decline in the fishery. This study was completed in 1923 and formed the subject matter of his doctoral thesis. In 1924 he was appointed to the staff of the Atlantic Biological Station as Ichthyologist and Assistant Director. His early work marked Dr. Leim as an enthusiastic naturalist, when following his shad work, he became interested in the life history of the shrimp, and the effect of light, temperature, salinity, and pH on certain copepods and mysids. He also carried forward an investigation of the smelt in various lakes and in the estuary of the Magaguadavic River, and cooperated in improving trout and salmon hatchery and fry planting methods. His interests in these fields were given little chance to develop at this time, for in 1926 he was appointed Assistant Director of the Board's Fisheries Experimental Station at Halifax. Here he became responsible for the direction of many investigations in the practical aspects of the fisheries. He personally carried out investigations on such problems as the prevention of drying in cold storage, the preparation of cod liver oil by freezing, the prevention of freezer burn during storage, and the smoking of fillets and haddies. He was closely associated with Dr. A. G. Huntsman in problems of rapid freezing of fish products and in the introduction of "quick frozen fillets" to Canadian markets. At Halifax he organized and directed courses over many years for hatchery officers, fishery inspectors

and fishermen. He also lectured in fisheries science at Dalhousie University, where he held the appointment of Associate Professor (1929–1946). During his Halifax years he was also for a time (1926–1929) editor of publications for the Biological Board.

In 1930 Dr. Leim was promoted to the position of Director of the Fisheries Experimental Station. He returned to the Atlantic Biological Station as Director in 1934, a position he held until 1941. During this period he again became associated with investigations in the general field of marine biology. He relinquished the position of Director in 1941, after which, as Chief Biologist, he gave his full attention to research on the fishes of the Canadian Atlantic. His investigations on the problems of various fisheries, hatchery problems, pollution, etc., form the subject matter of many internal reports, and record his broad interest and versatility. During 1944–1950 he was investigator in charge of the Atlantic herring investigations. Following the reporting and publication of the findings on herring, Dr. Leim turned his attention to the preparation of a book on the fishes of the Canadian Atlantic, notes for which he had been accumulating for many years. This work was approaching completion at the time of his death.

Those who worked closely under or with Dr. Leim appreciated his modesty and quiet dignity, his broad knowledge of the fisheries of the Canadian Atlantic, and his kindly sympathy with the problems of his staff and co-workers. He was ever ready with a helping hand.

Dr. Leim held membership in various scientific associations and societies. He took an active interest in the affairs of the Nova Scotian Institute of Science and was its President in 1933–34. Over the years, Dr. Leim was an ardent worker for the Canadian Red Cross Society and the Boy Scouts Association.

In 1931 Dr. Leim married Jean Jefferson Barnstead of Halifax, who survives him. Also surviving are a son, Alexander Henry Leim, jr., at home; a daughter, Mrs. Douglas G. Pittet, Toronto; and a granddaughter, Jennifer Pittet. His family, his associates on the staff of the Fisheries Research Board, and a host of friends mourn his passing.

NOTES

Trichodinids from the Gills of a New Host, the Lingcod *Ophiodon elongatus*

Trichodinids (Ciliata: Peritricha) are widely distributed in both marine and freshwater environments, where "the parasitic habit [of these protozoa] is highly developed in vertebrate associations, but grades toward commensalism with invertebrates; the majority of reported species are ectoparasitic upon the gills and body surfaces of various species of fishes where they feed upon desquamated epithelial cells and erythrocytes. Irritation from heavy infections may lead to hyperplasia, extravasation, secondary infection, and possibly to the death of the fish host" (Uzmann and Stickney, 1954). Uzmann and Stickney (1954) have summarized much data on the distribution of *Trichodina* and Davis (1947) has described many of the freshwater species. The wide distribution of trichodinids was further illustrated by Laird (1961) who found trichodinids on the gills of sculpins from the Nanaimo area. The present report extends the recorded host range of trichodinids to the lingcod (*Ophiodon elongatus*).

During October of 1960 there were excessive mortalities of "jigged" lingcod held in livewells in the Porlier Pass area (Vancouver Island) before slaughtering. The only affected tissue of recently dead and dying fish appeared to be the gills, which had blanched and yellow-green areas, particularly at the tips of the lamellae. Microscopically the gills of these fish showed evidence of capillary haemorrhage, much detritis with many spined diatoms embedded in the mucus (Bell, 1961) and trichodinids feeding on the gill epithelium (Fig. 2, 3). The protozoa were readily observed using a 10× objective and an 8× ocular, moving over the gill surfaces (Fig. 3). Further investigation showed that both freshly caught and captive specimens had trichodinids on the gills but no quantitative determination was made. Because the gills of all 25 fish examined from Porlier Pass and Departure Bay in 1960–61 were extensively infected, it is suggested that trichodinids are part of the indigenous gill fauna. We were unable to determine if these protozoa were the cause of death but their known destructive capabilities might suggest this. Debilitation of the host as a result of capture could well lead to increased intensity of infection.

No trichodinids could be found on the gills of freshly caught rock sole (*Lepidopsetta bilineata*) or butter sole (*Isopsetta isolepis*) from Departure Bay but a very few trichodinids were found on the gills of specimens which had been held in an aquarium during September and October. Perhaps trichodinids are actively parasitic on lingcod and commensals on rock sole and butter sole, or perhaps the trichodinids on the sole appeared as a result of the artificial con-

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ditions. Possibly also there is considerable variation and fluctuation in the number of trichodinids on the gills of any one species or individual, as was noted by Padnos and Nigrelli (1942) and others. All evidence suggests that there are large reservoirs of potential infection in the ocean, particularly among groundfish, and it would be of great interest to know the host range of trichodinids, the extent of cross infection and other epidemiological factors.

It would be of questionable value to attempt to identify the species of trichodinids found on lingcod unless the cells can be studied in uniprotozoan culture, because morphological criteria could not be assigned unequivocally to a single species. Furthermore, this paper is not primarily concerned with taxonomy. However, photomicrographs of single cells are shown in Fig. 1 and 3 in order to demonstrate the characteristic morphology of the trichodinids and to aid in the future identification of these protozoa.

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FIG. 1 "Side" view of a living trichodinid on a lingcod gill filament. A section of the striated band of the cell is seen just above the micron marker. This band on the posterior or aboral surface is part of the flexible adhesive disc which attaches to the host.

FIG. 2. "Side" view of a trichodinid (arrow) feeding on gill epithelium of freshly caught lingcod. Ellipse on the aboral surface is part of the adhesive disc.

FIG. 3. As Fig. 1 but illustrating further shapes and a moving trichodinid (arrow).

FIG. 4. A trichodinid from lingcod showing some characteristic features of the aboral surface as seen through the convex or adoral surface. The three concentric rings form the adhesive disc; the inner to the outer are the denticulate ring, the striated band and the border membrane. The ciliary girdle (locomotion) surrounds the cell. The cells can be observed conveniently by smearing a section of excised gill tissue on a slide and examining the accumulated fluid through a coverslip.

1
2
20μ
3
50μ

20μ
4

New Records for Occurrence of the White-tip Shark, *Pterolamiops longimanus* (Poey), and the Dolphin, *Coryphaena hippurus* L., in the Northwest Atlantic

A white-tip shark (*Pterolamiops longimanus*) was caught near the eastern edge of Georges Bank (Latitude 41°01′N, Longitude 65°54.5′W) on October 10th, 1961, from the Fisheries Research Board's research vessel *A. T. Cameron*. This shark was caught on a surface line trawl using mackerel as bait. The specimen was a male about 221 cm in total length and weighing about 140 pounds (64 kg). Identifying characters included the very short, compressed and well-rounded snout, the broadly-rounded tip of the first dorsal fin, the convex outline of the posterior margin of the lower caudal lobe and the distinctive white tips of the dorsal, pectoral and caudal fins. Proportional dimensions, expressed in percentage of total length, include: eye diameter 1.3, first dorsal base 10.3, second dorsal base 3.4, upper caudal lobe 28.2, lower caudal lobe 13.2, anterior margin pectoral 21.0, snout to first dorsal 31.6, and snout to second dorsal 64.0.

The specimen is noteworthy in that the area of capture is farther north than appears to have been reported previously for the western Atlantic. Bigelow and Schroeder (1948) reported the northern limit of distribution in the western Atlantic as Bahama Bank east of Florida. Subsequently, Schuck and Clark (1951) reported the capture of one specimen on June 12, 1950 in the Gulf Stream east of New Jersey and south of Newfoundland (Latitude 40°40.5′N, Longitude 57°01.5′W); while Backus *et al.* (1956) reported one caught southeast of Georges Bank on July 25, 1953 (Latitude 40°43′N, Longitude 66°39′W).

In the same area (Latitude 41°01′N, Longitude 65°54.5′W) where the white-tip shark was captured from the *A. T. Cameron*, and on the same date (October 10, 1961), 8 dolphins, *Coryphaena hippurus*, were caught with handlines. Sizes varied from 42 to 69 cm fork length (51–84 cm total length).

The occurrence of the dolphin as far north as Latitude 41° is undoubtedly rare. Vladykov and McKenzie (1935) recorded one specimen caught in Bedford Basin, Nova Scotia (ca. Latitude 44°30′N) on August 7, 1901. L. R. Day in a letter to Howard A. Schuck (Schuck, 1951) reported 3 specimens caught at North Rustico, Prince Edward Island (ca. Latitude 46°30′N) in 1945. Gibbs and Collette (1959) refer to these and to 4 additional records north of Cape Cod (ca. Latitude 41°40′N) which were originally reported by MacCoy (1931), Schuck (1951), Scattergood (1953), and Bigelow and Schroeder (1953).

Both the white-tip shark and the dolphin are tropical and subtropical in their distribution. The catches reported here probably reflect an unusual distribution of Gulf Stream water rather than a straying of these fish from their

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preferred habitat. Fishing was done immediately following the passing of a tropical hurricane (Hurricane Frances) and surface temperatures (22.9°C) and salinities (35.44‰) indicated an incursion of Gulf Stream water on to the eastern slope of Georges Bank.

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A Note Concerning the Origin and Quantitative Distribution of Acid-soluble Phosphorus Compounds and Free Sugars in Fish Muscle

Since the first recorded occurrence of acid-soluble phosphorus compounds (Tarr, 1950) and of ribose and glucose (Tarr, 1953; 1954) in fish muscles, work in this field has proceeded actively in several countries, and has been greatly facilitated by improved analytical techniques. The purpose of the present Note is to outline briefly the results obtained in a recent investigation of certain phases of this general problem at this Station (Tarr and Leroux, 1962).

Good separation of the principal nucleotides (adenosine mono-, di- and triphosphate, inosinic acid, and di- and triphosphopyridine nucleotide) and sugar phosphates (glucose 1- and 6-phosphates, fructose 6-phosphate and fructose 1,6-diphosphate) was achieved by absorption of potassium hydroxide neutralized cold 0.6*M* perchloric acid extracts of fish muscles on Dowex 1×4 chloride ion exchange resin columns. The compounds were eluted and separated by a combination of increasing chloride and decreasing pH gradients, "complexing" with borate ions and buffering with acetate ions. Where positive identification of compounds was necessary they were isolated as lithium or barium salts.

It was found that radioactive glucose (uniformly labelled C^{14}), when introduced intravenously into live sockeye salmon or rainbow trout, entered the Embden–Meyerhof glycolytic pathway, since intermediates such as lactate and the hexose phosphates became radioactive. When radioactive glycogen (prepared from salmon muscle) was introduced into fish muscle post mortem, it was degraded both by the Embden–Meyerhof pathway (radioactive hexose phosphates were isolated) and by an amylolytic pathway (radioactive maltose and glucose were isolated). Only a very small fraction of the glucose was formed by hydrolysis of glucose 6-phosphate. Results of the above studies showed that neither ribose 5-phosphate nor free ribose is formed via the hexose monophosphate shunt pathway.

When uniformly labelled C^{14}-adenosine triphosphate was introduced into fish muscle, radioactive inosinic acid and ribose were formed post mortem. The hexose phosphates and glucose were not radioactive. This, when considered in conjunction with data previously published from this Station, makes it almost certain that all free ribose in fish muscles arises through post-mortem degradation of adenosine triphosphate (or other nucleotides) and nearly all the glucose from amylolytic cleavage of glycogen.

It has been found that all, or practically all, the fructose monophosphate which occurs in muscles of such widely divergent species as Atlantic cod and Pacific salmon is fructose 6-phosphate. No fructose 1-phosphate was identified

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by paper chromatography or by attempts to determine acid-labile phosphorus. Pentose phosphates were not found in muscle of freshly killed fish, but small amounts were formed post mortem. No ribose 1-phosphate was found and it was demonstrated that this very acid-labile ester is largely or entirely destroyed during extraction of the muscle with 0.6*M* perchloric acid at 0°C. The results, so far as inability to demonstrate fructose 1-phosphate and ribose 1-phosphate in fish muscle are concerned, are in direct opposition to the recent findings of other investigators (Burt and Jones, 1961; Burt, 1961).

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